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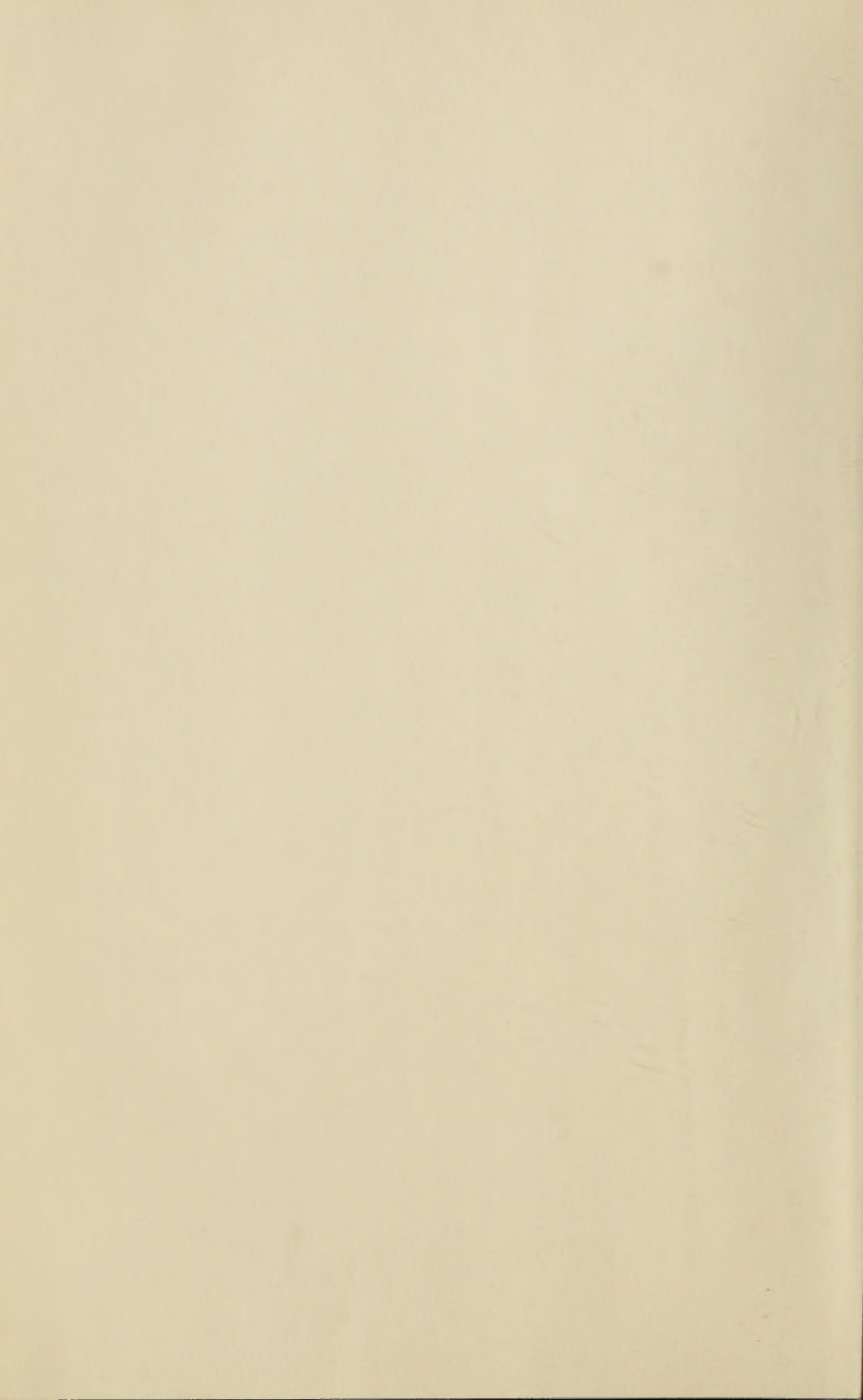
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SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 149, NUMBER 1

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Charles D. and Mary Vaux Walcott  
Research Fund

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THE DISTRIBUTION AND ABUNDANCE  
OF FORAMINIFERA IN  
LONG ISLAND SOUND

(WITH FOUR PLATES)

By  
MARTIN A. BUZAS

U. S. National Museum  
Smithsonian Institution



(PUBLICATION 4604)

CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION  
MAY 25, 1965

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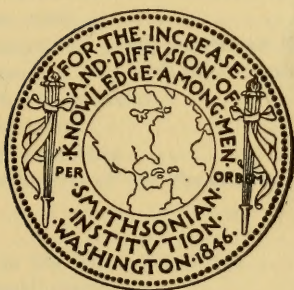
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# CONTENTS

	Page
Introduction .....	1
Purpose and location.....	1
Acknowledgments .....	1
Previous work .....	2
Oceanography .....	2
Sediments .....	3
Studies of Foraminifera.....	4
Methods of study.....	4
Field work .....	4
Laboratory work .....	6
Significance of a foraminiferal sample.....	7
Introduction .....	7
Statistical significance of species proportions.....	8
Statistical significance of numbers of individuals.....	10
Statistical significance of numbers of individuals as related to the wet volume of samples .....	11
Summary of the significance of a foraminiferal sample.....	11
Distribution of the Foraminifera.....	11
General aspects of the fauna.....	11
Distribution of the living population.....	13
Size of the living population.....	21
Zonation of the living population.....	21
<i>Elphidium clavatum</i> zone.....	22
<i>Buccella frigida</i> zone.....	22
<i>Eggerella advena</i> zone.....	22
Comparison of the number of living individuals in traverses 2 and 3...	24
Comparison of the standing crop with other areas.....	26
Distribution of the total population.....	27
Size of the total population.....	32
Zonation of the total population.....	36
Summary of the distribution of the Foraminifera.....	36
Seasonal samples .....	38
Introduction .....	38
Seasonal variations in the living population.....	39
Significance of seasonal samples.....	41
Summary of seasonal samples.....	43
The Foraminifera in relation to the sediments.....	43
Foraminifera in short cores.....	43
Particle-size analyses .....	44
Significance of particle-size analyses.....	47
Ratios of living to total populations in L.I.S.....	48
Significance of environmental factors.....	50
Paleoecologic implications .....	53
Systematic catalog of species.....	54
General Summary .....	63
References .....	86



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BY MARTIN A. BUZAS  
*U. S. National Museum  
Smithsonian Institution*

(WITH FOUR PLATES)

## INTRODUCTION

### PURPOSE AND LOCATION

This study is a quantitative survey of the benthonic Foraminifera in Long Island Sound. Its purposes are: 1, To ascertain the distribution and abundance of the living population; 2, to discover any seasonal variation in the living population; 3, to investigate the relationship between particle size of the sediment and foraminiferal distribution and abundance; 4, to ascertain the distribution and abundance of the total (living plus dead) population and compare it with that of the living population; 5, to attempt to relate the observed foraminiferal distribution and abundance to environmental factors.

Long Island Sound <sup>1</sup> is a partially enclosed body of water with an area of about 930 square miles. Its location and configuration are shown in figure 1. In the central portion maximum depths of about 40 m. are found about 4 nautical miles from the Long Island shore. At a comparable distance from the Connecticut shore the water is less than 20 m. deep. Mixing with the more oceanic waters of Block Island Sound occurs through the eastern passage. In the narrow western portion a limited amount of exchange takes place with the waters of New York Harbor.

### ACKNOWLEDGMENTS

I wish to thank Dr. K. M. Waage for his valuable advice, encouragement, and supervision of the study. To Dr. G. A. Riley, who of-

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<sup>1</sup> Referred to hereafter as L.I.S.

ferred many helpful suggestions and able assistance in the field, I owe my sincere thanks. Capt. H. Glas of the *Shang Wheeler*, a research vessel of the U. S. Fish and Wildlife Service at Milford, Conn., was most helpful in the field. Thanks are due also to Dr. A. McCrone, who arranged for a cruise aboard a New York University research vessel in July 1961. Dr. H. Seal kindly gave advice on statistical methods, and Dr. J. E. Sanders placed some valuable equipment at the writer's disposal. Ruth Todd and Dr. J. F. Mello's constructive criticism of the manuscript was most helpful. The Foraminifera were illustrated by Lawrence B. Isham, scientific illustrator, U. S. National Museum. Figured specimens are deposited at the U. S. National Museum.

The research was supported in part by grants from the Sigma Xi-RESA Research Fund and the Schuchert Fund of Yale Peabody Museum.

#### PREVIOUS WORK

#### OCEANOGRAPHY

One of the reasons why L.I.S. was chosen for the present study is that it is a relatively well known body of water. Riley (1952) studied the hydrography of Long Island and Block Island Sounds. Riley and others (1956 and 1959) have studied the physical and chemical oceanography as well as some of the flora and fauna of L.I.S. Some aspects of their work pertinent to the area of the present study are described below.

*Temperature.*—The temperature ranges from a minimum of about 2°C. in midwinter to a maximum of about 25°C. in late summer. The temperature gradient from surface to bottom is nearly vertical from August to March, whereas a negative gradient, not exceeding 5°C., is present from March to August.

*Salinity.*—The salinity varies from a spring minimum of about 25‰ to an autumn maximum of 29‰. Because the effect of fresh-water drainage is more pronounced in the narrow western portion, it is often 3‰ fresher than the central area. The salinity between top and bottom water usually varies not more than 1‰. Fresh-water drainage into L.I.S. is mainly from the Connecticut drainage basin; this fresh water moves eastward and out of L.I.S., being replenished by bottom water entering from Block Island Sound.

*Oxygen.*—Minimum values for oxygen are found in summer. During autumn and winter oxygen is just slightly undersaturated from the surface to the bottom. The minimum values for bottom water are



40 percent of saturation in the western end and 50 percent of saturation in the central portion.

*Phosphate*.—Maximum concentrations of phosphate occur in autumn and winter, whereas minimum concentrations are found in summer. The phosphate level is higher in the western end especially during the autumn and winter. Phosphate appears not to be an important limiting factor for phytoplankton growth in the central basin.

*Nitrate*.—Maximum concentrations of nitrate occur in autumn and early winter. Concentrations are greater in the western area during the maximum. During the remainder of the year, however, there is little nitrate anywhere in the column. Enrichment experiments have shown that nitrogen is probably an important limiting factor for phytoplankton growth in the central basin.

*Phytoplankton*.—A midwinter flowering with a peak between January and March occurred each year in which L.I.S. was studied. This is normally followed by several irregular summer flowerings of moderate size. In the autumns of 1954 and 1955 there were marked flowerings, whereas none occurred in 1952 and 1953. Illumination, stability of the water column, and nutrient supply were suggested to explain these differences. The amount of chlorophyll in the water column increased progressively from east to west.

*Zooplankton*.—The seasonal cycle for the zooplankton showed maxima in late spring and late summer, with a minimum occurring in midwinter. There appeared to be no large regional differences in zooplankton concentrations even though the western end could potentially support a larger crop.

*Particulate matter*.—Measurements of the total particulate matter, organic matter, and chlorophyll in surface water at a station in central L.I.S. indicated that although there was a 20-fold variation in chlorophyll during the year, the organic matter varied within narrow limits. This suggests that at times much of the organic matter occurs as detritus or as organisms that contain very little chlorophyll. About two-thirds of the total particulate matter is composed of nonliving material.

#### SEDIMENTS

McCrone and others (1961) studied the sediment in selected samples from 23 traverses in L.I.S. They reported silt as the most common sediment and indicated a general increase in grain size toward near-shore sands. The pH of the silts in the tops of 17 cores

had a range of 7.6-6.8. The Eh values were all negative, and  $H_2S$  was detected in all the silt samples reported. The total organic hydrocarbon content of selected samples was about 0.1 percent. X-ray diffraction analyses indicated the most common minerals are: Quartz, muscovite, biotite, albite, microcline, kyanite, augite, hornblende, chlorite, calcite, and dolomite. Some observations on Foraminifera, corals, mollusks, spores and pollen, and diatoms were reported.

#### STUDIES OF FORAMINIFERA

Shupack (1934) reported eight species of Foraminifera from six sediment samples taken in New York Harbor. The most abundant constituents were members of the genus *Elphidium*.

Parker (1952b) studied the distribution of the Foraminifera in the Long Island Sound-Buzzards Bay area. She defined the following three foraminiferal facies in the area: Facies 1—confined to the Housatonic and Connecticut Rivers; facies 2—found in L.I.S., Buzzards Bay, and Gardiners Bay; facies 3—found in Block Island Sound and southwest of Cuttyhunk. Facies 1 is composed for the most part of arenaceous species typical of estuarine and marsh environments. Facies 2 and 3 are composed mainly of calcareous forms. A few species are restricted to either facies 2 or 3, and the relative abundance of species differs in the two facies. *Elphidium incertum* was the most abundant form in facies 2. Parker listed 36 species from L.I.S., of which 7 were indicated as persistent in their occurrence.

Charmatz and McCrone (1961) listed 22 species of Foraminifera from L.I.S. They indicated that species of *Elphidium* are most abundant.

#### METHODS OF STUDY

##### FIELD WORK

A total of 220 samples were obtained from 130 stations occupied during 14 cruises. Most of the stations are located in north-south traverses which are numbered 1 through 5 from west to east (fig. 1). The traverses are spaced about 10-14 nautical miles apart. The first and last stations in each traverse were located alongside buoys or within sight of known shore positions. The stations between were located about 1 nautical mile apart along a north-south bearing. Traverse 3, which is located at about the geographic center of L.I.S., was sampled seasonally. Since only the first and last stations could

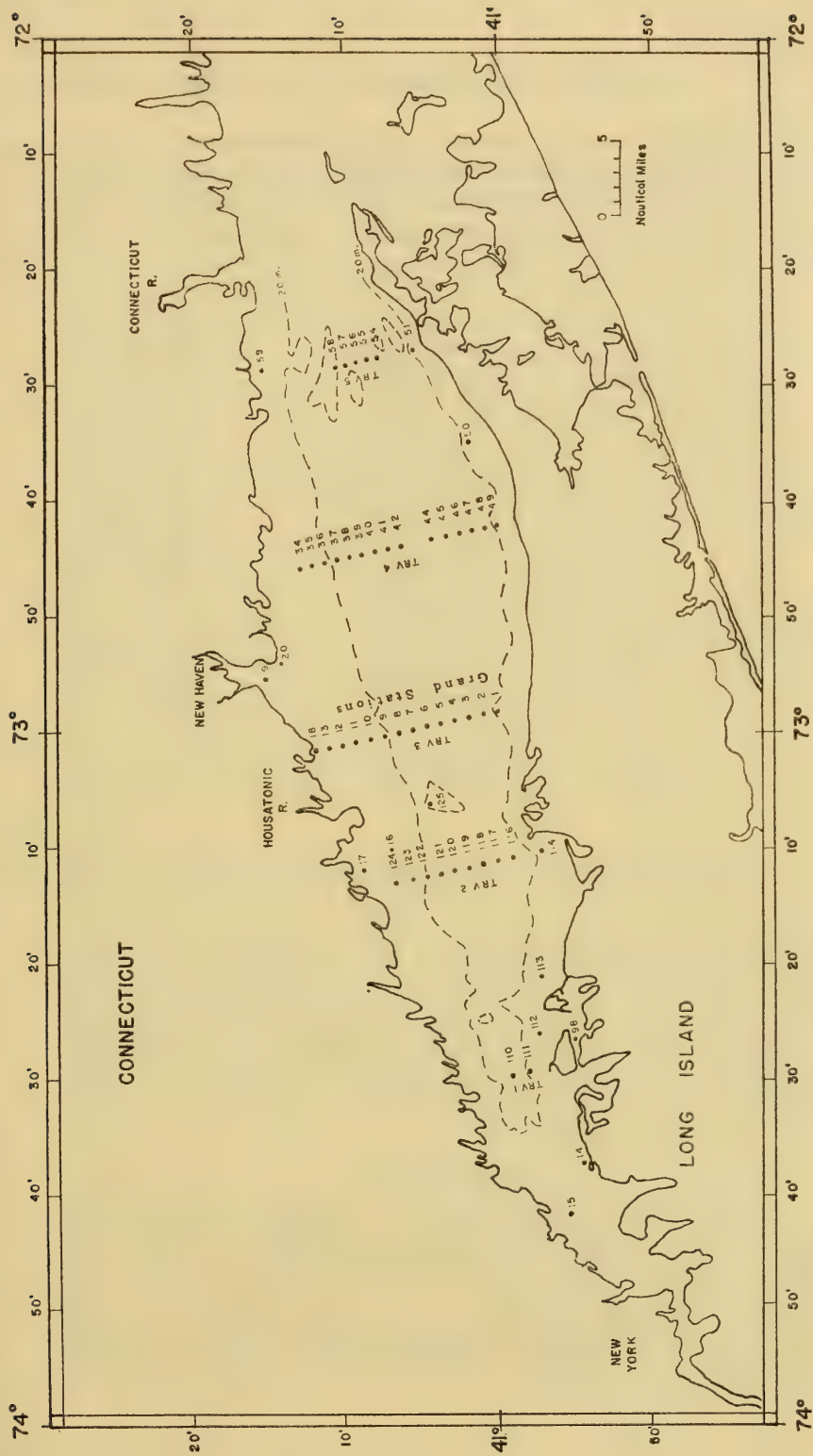


Fig. 1.—Location of traveres and stations in Long Island Sound.

be located accurately, the seasonal samples between were given different station numbers. The station numbers (1-13) shown in figure 1 for traverse 3 are plotted from the first time the traverse was sampled. The traverses, sampling times, and station numbers are as follows:

Traverse	Time	Stations
1 .....	Nov. 19, 1962	110, 111
2 .....	Nov. 19, 1962	114-124
3 .....	June 6, 1961	1-13
3 .....	Oct. 3, 1961	1, 33-22, 13
3 .....	Jan. 15, 1962	71-60, 13
3 .....	Mar. 24, 1962	84-73, 13
3 .....	June 12, 1962	97-86, 13
3 .....	Sept. 26, 1962	109-100, 13
3 .....	Nov. 20, 1962	126-135, 13
4 .....	Nov. 7, 1961	49-34
5 .....	Nov. 7, 1961	51-58
Miscellaneous Stations .....	July 15, 1961	15, 14
" " .....	Aug. 7, 1961	16, 17, 19, 20
" " .....	Aug. 24, 1961	18, 19
" " .....	Nov. 7, 1961	50, 59
" " .....	Jan. 9, 1962	13
" " .....	June 13, 1962	98
" " .....	Nov. 19, 1962	113, 112
" " .....	Nov. 20, 1962	125

Most of the stations were sampled by means of a small coring tube 3.5 cm. in diameter. A few centimeters of water above the sediment water interface and the top centimeter of the core were placed in a jar with neutralized formalin at the time of collection. The second centimeter of the core was removed for particle-size analysis. At those near-shore stations that have a sandy bottom a snapper-grab sampler was used. About 10 ml. of wet sediment was removed from it and preserved for foraminiferal analysis. An additional 10 ml. was obtained for particle-size analysis.

#### LABORATORY WORK

The pH of the preserved samples was checked periodically. None of the samples became acidic during the duration of their storage. When the sediment in a sample jar had settled sufficiently, the sediment level was marked with tape. The biological stain Rose bengal, the properties of which are discussed by Walton (1952), was added the day before examination of the material. After staining, the



sample was washed in a bank of sieves having openings of 125 and  $62\mu$ . The two fractions were then placed in petri dishes under which were fastened grids drawn on black cardboard. The "living" (those Foraminifera which contained protoplasm at the time of collection as indicated by the stain) and "dead" (empty tests) populations were then counted while wet. The wet volume of each sample was measured by refilling the sample jar to the tape level with water and decanting into a graduated cylinder. This procedure was repeated four times and the values averaged. At a few near-shore stations the number of dead individuals was well over 1,000, and in these samples only the living population was counted wet. The sample was then dried and a flotation method using  $\text{CCl}_4$ , described by Cushman (1948), was used to concentrate the tests. The sample was then aliquoted using a microsplit described by Skolnick (1959), and the dead population was estimated from the fraction counted.

Particle-size analyses were made on 59 stations. The methods used were essentially those described by Krumbein and Pettijohn (1938). After removal of electrolytes by decantation, the sediment was wet-sieved into fractions coarser and finer than  $62\mu$ . The coarse fraction was then given a standard Ro-tap sieve analysis. The fine fraction was dispersed in a N/100 solution of sodium oxalate and agitated on a milk-shake machine for 10 minutes before being given a pipette analysis.

## SIGNIFICANCE OF A FORAMINIFERAL SAMPLE

### INTRODUCTION

Some of the objectives of a quantitative study of foraminiferal populations in a given area are: 1, To establish the relative abundance with which various species are distributed; 2, to compare the relative abundance of living and dead populations; 3, to estimate the standing crop or number of living Foraminifera per unit area; 4, to estimate the number of living Foraminifera seasonally, which will also give a better estimate of 3; 5, to estimate the number of dead Foraminifera per unit area so that a living to total (L/T) ratio can be calculated as an indicator of relative rates of sedimentation.

In order to accomplish these ends an undisturbed sample of known surface area and volume must be obtained. Phleger (1951) used a small plastic core liner which has an inner diameter of 3.5 cm. ( $1\frac{3}{8}$  inches). He sampled the surface water immediately above the core and the top centimeter of the core for his foraminiferal analysis. Since then other workers have adopted this method of



sampling when sediment type permits. Walton (1955) discussed the advantages of using equal wet volumes rather than dry sediment weights in foraminiferal ecology.

A sample is assumed to be representative of both the distribution and abundance of the foraminifers at the sampling site (station) as well as of the total area the sample represents. Phleger (1952) has indicated that in the Gulf of Maine the foraminiferal samples are representative of the total area a sample represents because the distribution of species is not haphazard, has localized centers or highs, and decreases away from these highs in an orderly manner. Walton (1955) discussed the same problem in his study of Todos Santos Bay, Calif. The percentage distributions of the living species in the Bay indicated the highest rate of variation at depths of less than 50 fathoms. In deeper water the amount of fluctuation diminishes. Because of the stability of the percentage distribution of species in deeper areas, Walton concluded that his sampling grid was giving an adequate representation of foraminiferal distribution.

In L.I.S. the percentage distribution of foraminiferal species is meaningful and repeatable. This suggests that the samples from the Sound are representative of the foraminiferal distribution in the area. In order to test the reliability of a sample at a station at a particular time, 12 pairs of samples were taken at various locations. Each member of a sample pair was taken within minutes of the other, by the same method, and at the same location as far as conditions would permit. Theoretically, each pair should be identical. Sample pairs 14-14' and 125-125' were grabs, all the rest were cores. In the pair 14-14' the dead population was estimated.

#### STATISTICAL SIGNIFICANCE OF SPECIES PROPORTIONS

The species proportions in the sample pairs will now be compared. The data are viewed most conveniently by arranging them in a contingency table (see table 1, page 65). A qualitative approach would be to compare visually the number of individuals in each species of a sample pair and decide arbitrarily whether or not the species proportions are similar. If the species proportions differ widely, then the samples are considered not homogeneous. A more quantitative approach is to choose a statistic which will test for homogeneity of sample pairs. In the present study the statistic chosen was chi-square. Because one of the assumptions on which this statistic is based is violated if the frequency in a given category is too small, only the three most abundant species were used in making the calculations.

These species are: 1, *Elphidium clavatum*; 2, *Buccella frigida*; and 3, *Eggerella advena*. In the pair 59-59' *Elphidium tisburyense* was substituted for the missing *Eggerella advena*. Table 1 shows the results of the calculations for the living and total populations of the three abundant species in the 12 sample pairs. Even though only the most abundant species were used in the calculation of chi-square, in some sample pairs the expected frequency in a given cell was less than two. In these cases, the species with the low expected value was deleted from the calculation of chi-square. In the living populations of the sample pairs 102-102', 106-106', and 108-108' two of the three abundant species have expected frequencies of less than two and therefore chi-square was not calculated in these instances. The degrees of freedom for chi-square when three species are used in its calculation is two; when two species are used, it is one. The 95-percent level was chosen as significant. A significant value of chi-square indicates the samples are not homogeneous.

Looking at the results we do not find a significant value of chi-square for the living population in six of the nine sample pairs tested. The sample pairs 10-10', and 24-24' give a significant value of chi-square. The pair 14-14' was a near-shore grab, and other near-shore grabs (not shown in table 1) taken a week apart also indicate a wide degree of fluctuation. The pairs 10-10' and 24-24' are actually from the same area sampled at different times. This station (18 m. depth) is located in a transition zone between the clearly near-shore and offshore faunal assemblages. The pair 59-59' is a near-shore core which did not give a significant value of chi-square. The pair 125-125', however, is a grab from the center of L.I.S. and it also did not give a significant chi-square value. The effect of sampling method, therefore, is not clear, although for reasons already discussed an undisturbed sample from a core is certainly more desirable. In general, we may conclude that in the living population the proportions of the species investigated are homogeneous in the sample pairs from the offshore area.

In the total population 7 of the 12 sample pairs yielded a significant chi-square value. They are the pairs 10-10', 14-14', 24-24', 102-102', 108-108', 125-125', and 129-129'. Curiously, the pair 102-102' is from the same station (sampled at still another time) as the pairs 10-10' and 24-24'. We may conclude that in the total population the proportions of the three species investigated are homogeneous in four of the seven sample pairs from the offshore area.

## STATISTICAL SIGNIFICANCE OF NUMBERS OF INDIVIDUALS

I have suggested, however, that it is desirable not only to establish the relative abundance (species proportions) of the foraminiferal population in a given area, but also to estimate the actual number of individuals living and/or dead per unit area. To do so, it must be assumed that the number of individuals in a given sample is a representative portion of an unknown population which is homogeneously distributed throughout the area the sample represents.

If each member of a sample pair is a reliable estimate of the number of individuals at a station, then a sample pair should be from the same statistical population. Let the total number of individuals in a sample pair be  $n$ . The probability of any individual belonging to one or the other sample is  $p$  and  $q = 1-p$  respectively. Therefore, we have a binomially distributed variate with a mean of  $np$  and a variance of  $npq$ . When  $n$  is large and  $p$  is close to  $\frac{1}{2}$ , the binomial distribution closely approximates the normal distribution. The transformation is achieved by the formula:

$$x = \frac{(r - np) - \frac{1}{2}}{\sqrt{npq}},$$
 where  $x$  is the standardized normal random variable,  $r$  is the number of individuals in a sample, and  $\frac{1}{2}$  is a correction for continuity. (Bradley, 1960, gives a discussion of tests based on the binomial distribution.)

The value of  $x$  was calculated for the total and living populations in all the sample pairs. The results are shown in table 2 (page 71). If a sample pair has a significant value of  $x$ , then we are confident that each member of the pair is from the same population. In the living population, 7 of the 12 sample pairs have a significant  $x$  value. In the offshore areas (pairs 104-104' through 133-133'), 5 of the 7 pairs give a significant  $x$  value. In the total population, 5 of the 12 pairs have a significant  $x$  value, while in the offshore areas 3 of the 7 pairs are significant. In general, the number of living individuals in the sample pairs give better results than the total number, and the offshore areas give a more reliable estimate of the number of individuals at a station than the near-shore areas.

The possibility that the Foraminifera in L.I.S. are not homogeneously distributed throughout the area that a sample represents has not been thoroughly investigated. As will be seen later, however, in the offshore areas, the number of living individuals in samples from the same traverse does not differ significantly.



STATISTICAL SIGNIFICANCE OF NUMBERS OF INDIVIDUALS  
AS RELATED TO THE WET VOLUME OF SAMPLES

The sediment-water interface in most parts of L.I.S. is a transitional boundary. When a few centimeters of water above the core are decanted, often much of it is sediment-laden. The actual wet volume then is variable even though care is taken to remove only 1 cm. of core. Therefore, the wet volume was determined for all samples. The number of individuals in the living and total populations of the sample pairs was corrected to a wet volume of 10 ml. The value of  $x$  was then calculated for the corrected number of individuals in the living and total populations. The results are shown on the right side of table 2. The values of  $x$  that were significant in the original sample pairs remained so. In addition, the corrected number of living individuals in the pairs 102-102' and 129-129' as well as the corrected number of total individuals in the pairs 10-10' and 104-104' became significant. The reward hardly seems to justify the effort, and for practical purposes the samples can be considered to be of equal volumes without any serious error.

## SUMMARY OF SIGNIFICANCE OF A FORAMINIFERAL SAMPLE

In summary, the analyses of 12 paired samples indicates:

1. The proportions of the species investigated are more homogeneous in the living population than in the total population.
2. The number of living individuals at a station can be more reliably estimated than the total number of individuals.
3. The offshore areas are more homogeneous and the number of individuals at a station can be more reliably estimated than in the near-shore areas.
4. Samples can be considered to be of equal volume without any serious error.

## DISTRIBUTION OF THE FORAMINIFERA

Conclusions regarding the distribution of the Foraminifera are based on population counts made on 161 samples from 130 stations. Table 3 (page 72) tabulates the percent of each species in the living (L) and total (T) populations at each station.

## GENERAL ASPECTS OF THE FAUNA

Twenty-three species belonging to fifteen genera were found in L. I.S. Most of the species have living representatives, but the species

*Ammoscalaria* cf. *fluvialis*, *Trochammina inflata*, *T. lobata*, and *Nonionella atlantica* are represented only by empty tests. No planktonic Foraminifera were found.

Parker (1952b) recorded 36 species from L.I.S. Of these only 19 were found in the present study. The species *Eggerella advena*, *Elphidium incertum* (*E. clavatum* of this study), *E. subarticum* (*E. pauciloculum* of this study), *Eponides frigidus* var. *calidus* (*Buccella frigida* of this study), *Nonion tisburyensis* (*Elphidium tisburyense* of this study), *Reophax dentaliniformis*, and *Trochammina squamata* were listed as persistent in occurrence by Parker. All these species were commonly found in the present investigation.

In the present study the species *Elphidium clavatum*, *E. pauciloculum*, *E. varium*, *Buccella frigida*, and *Eggerella advena* usually make up about 90 percent of the total as well as of the living population. Of these, however, *E. clavatum*, *B. frigida*, and *E. advena* are most abundant and commonly comprise over 75 percent. Parker (1952b) indicated the most abundant species in her facies 2 (L.I.S., Buzzards Bay, Gardiners Bay) were *E. advena*, *E. incertum*, *E. subarticum*, and *E. frigidus* var. *calidus*. There is, then, with the exception of *E. varium*, complete agreement. *E. varium* was probably included under *E. incertum* and *E. subarticum* by Parker because this species closely resembles these forms.

The duplicate study of this area is instructive in that it shows that caution must be used when considering the significance of the number of species in a given area. On the other hand the more abundant species are, as one would hope, abundant in both cases. The number of genera also seems to be less variable. Parker found 19, whereas 15 were found by the writer.

Parker (1952b) was able to differentiate between the fauna of L.I.S. and Block Island Sound. She found that some species such as *Reophax dentaliniformis* and *R. nana* are restricted to L.I.S. In addition she found that the fauna in L.I.S. contained a very large percentage of *Elphidium incertum*. Parker (1952b, p. 438) indicated that in the central part of L.I.S. there is a decrease in the percent of this species. Therefore, with the exception of *E. varium*, there is complete agreement between the faunal composition noted by Parker and that noted during my investigation.

Using Parker's data, the average number of species per station in L.I.S. is 8 (7 were found in the present study), whereas in Block Island Sound it is 14. The waters of Block Island Sound are more oceanic in character, having a higher salinity and less variation in



temperature than the more restricted waters of L.I.S. On the average, stations in L.I.S. have fewer species and greater dominance by a single species than the more open-ocean waters of Block Island Sound.

In the total population 10 species were found in traverse 1, 13 in traverse 2, 14 in traverse 3, and 19 in traverse 4. In the living population the number of species in the traverses are 8, 10, 12, and 14 respectively. The increase of species to the east is probably due to two factors, namely, migration into L.I.S. by open-ocean species would take place from that direction, and there is an increase in salinity of 3-5‰ from west to east.

#### DISTRIBUTION OF THE LIVING POPULATION

Frequency distributions were drawn for the percent of all the common species, but only the distributions for *Elphidium clavatum*, *Buccella frigida*, and *Eggerella advena* show a consistent pattern. Traverse 3 was sampled at seven different times, and the three abundant species show the same pattern over and over again. In order to present the data concisely, the 88 seasonal stations taken in traverse 3 were grouped into 13 "grand" stations. Table 4 (page 80) shows the correlation of the seasonal stations with the grand stations. The number of individuals of each species from the seasonal stations in a grand station were added and the percent distribution calculated.

Figure 2 shows the distribution of *B. frigida*, *E. advena*, and *E. clavatum* in percent of the living population for the 13 grand stations of traverse 3. Station 1, which is composed of coarse sand (Md  $\phi$  0.8), is about  $1\frac{1}{2}$  nautical miles off the Long Island shore. It was sampled three times and yielded only five foraminifers. The remaining stations (2-13) are about 1 nautical mile apart in a northerly direction. It should be emphasized that the same pattern shown in figure 2 was observed each time traverse 3 was sampled.

Traverse 2 is about 10 nautical miles west of traverse 3. Stations 114-124 are located about 1 nautical mile apart from south to north respectively. No sample was obtained at station 115. The same pattern observed in traverse 3 is repeated in traverse 2 and is shown in figure 3.

Traverse 4 is located about 14 nautical miles east of traverse 3. Stations 34-48 are located about 1 nautical mile apart from north to south respectively. Figure 4 shows the distribution of the abundant species.

Traverses 2, 3, and 4 all show the same general pattern. The north-

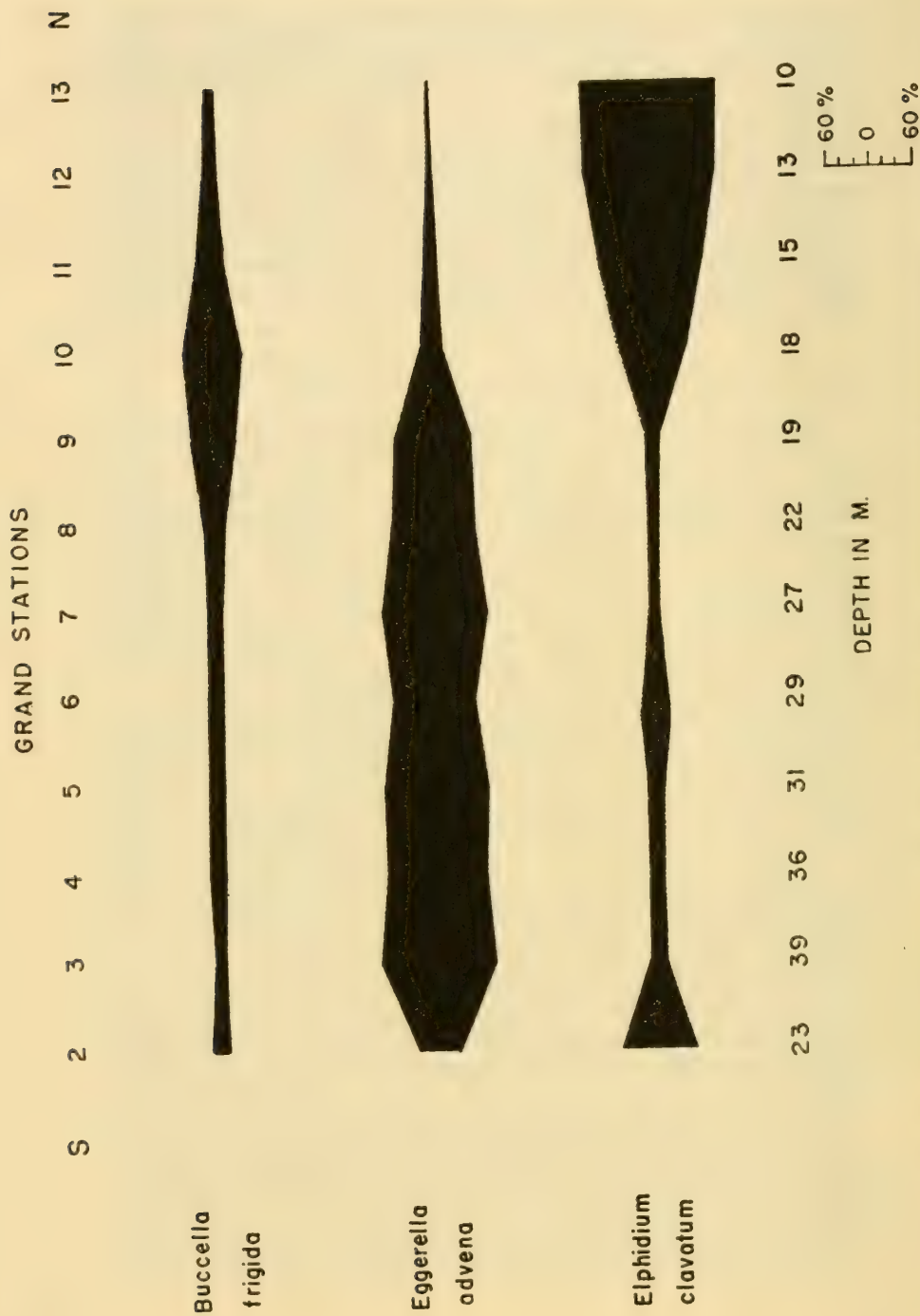


FIG. 2.—Distribution of abundant species in percent of the living population at grand stations of traverse 3.

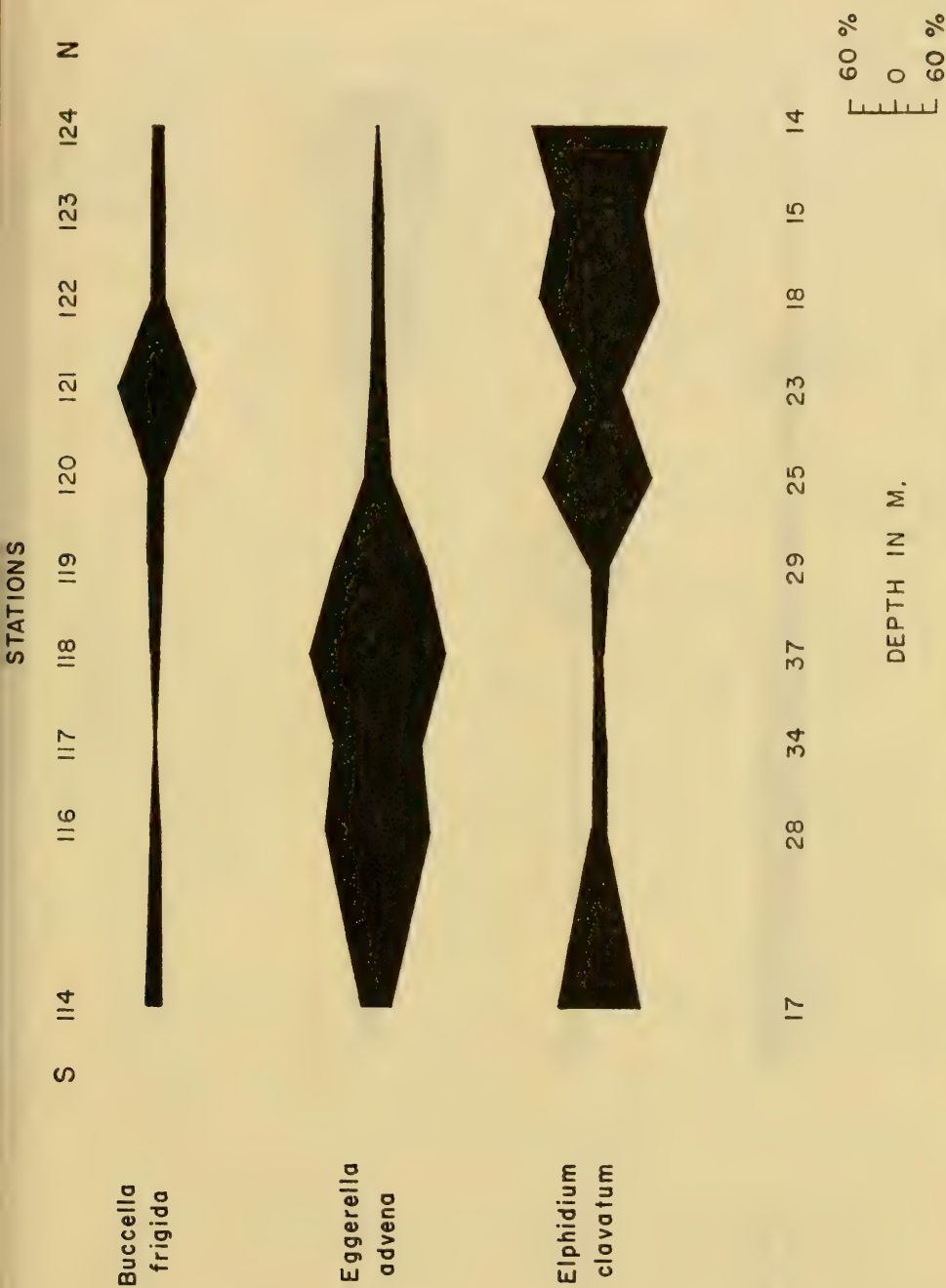


FIG. 3.—Distribution of abundant species in percent of the living population at stations of traverse 2.

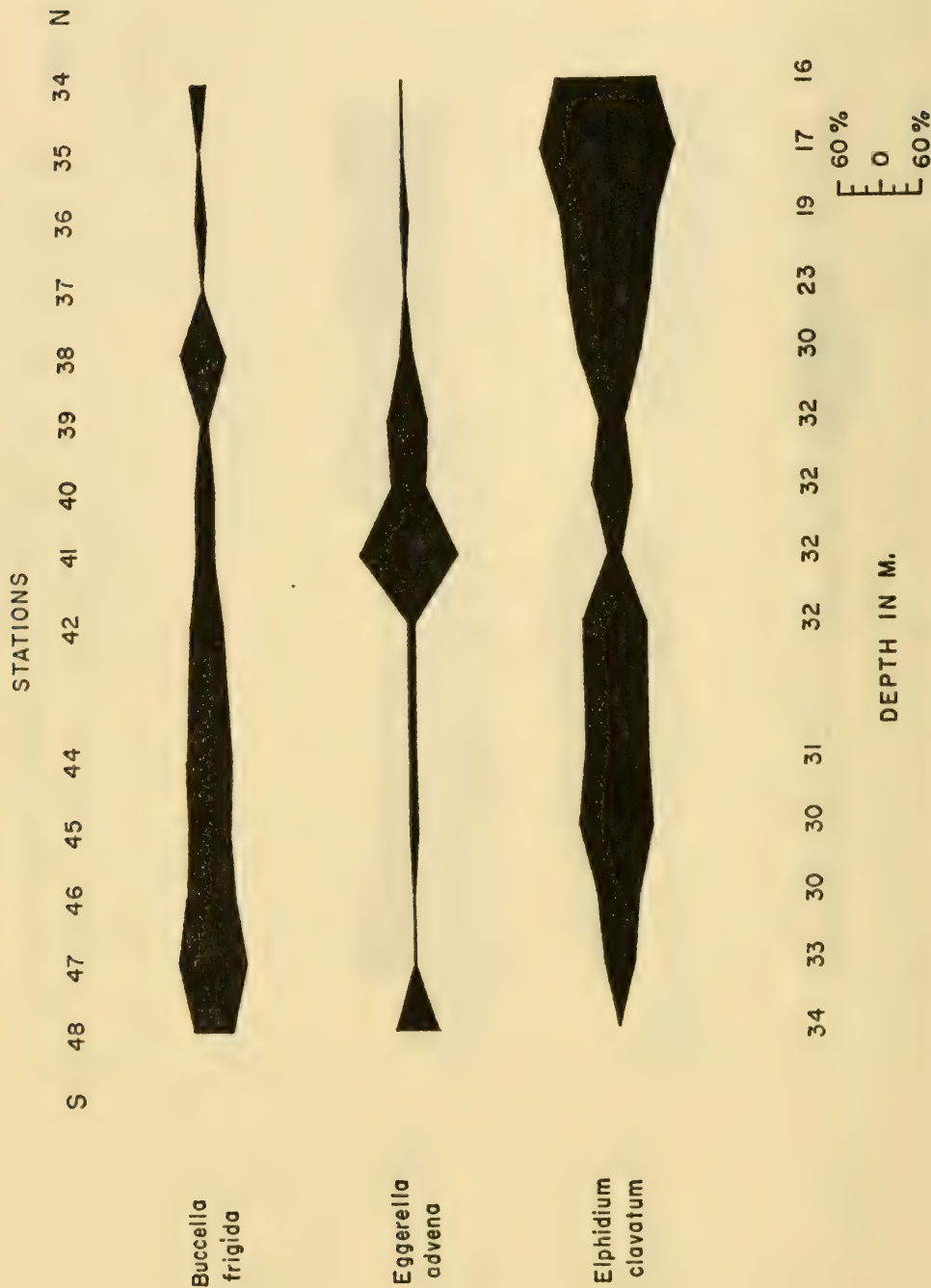


FIG. 4.—Distribution of abundant species in percent of the living population at stations of traverse 4.

ern end of a traverse always has a very high percentage of *E. clavatum*, which diminishes as *B. frigida* becomes more abundant and reaches a maximum 4 or 5 nautical miles from the Connecticut shore. As the percent of *B. frigida* decreases, *E. advena* increases and dominates the central area. At the southern end of the traverses there is a suggestion of another increase in the relative abundance of *B. frigida* and *E. clavatum*, but symmetry is not achieved. *E. advena* is not nearly as well developed in traverse 4 as it is in the other two traverses.

Traverse 5 is located about 12 nautical miles east of traverse 4. It includes stations 51-57 from south to north respectively. Foraminifera are very rare in this traverse. A few living individuals belonging to the species *Trochammina squamata* and *Poroeponides lateralis* were observed.

Traverse 1 is located about 14 nautical miles west of traverse 2. It consists of stations 110 and 111. Table 3 (page 72) shows that these stations have a percentage distribution of species similar to the stations in the central areas of the other traverses.

The areal distribution of *Elphidium clavatum* in percent of the living populations is shown in figure 5. About 3 to 4 nautical miles from shore at depths of less than 20 m., *E. clavatum* usually comprises over 70 percent of the living population. In very shallow water the abundance of this species increases to over 90 percent. *E. clavatum* is abundant in near-shore areas on both sides of the Sound but is not found in the near-shore area of Long Island east of longitude 73°10'. This latter area is composed of coarse quartz sand, and almost no foraminifers were found there except at station 50. In the central areas of L.I.S., *E. clavatum* occurs with much lower frequencies. In traverse 2 its minimum occurs farther south than in traverse 3 and 4.

The areal distribution of *Buccella frigida* in percent of the living population is shown in figure 6. In traverses 1 and 2 its maximum is confined to a narrow band north of center. In traverse 3, however, this species becomes more abundant, and farther east in traverse 4 it commonly comprises over 20 percent of the living population.

The areal distribution of *eggerella advena* in percent of the living population is shown in figure 7. This species has an almost symmetrical distribution pattern. It reaches a maximum of over 70 percent in the central area and decreases in relative abundance toward the north and south. In traverse 4, *E. advena* occurs with very low frequencies south of its maximum. This species is absent from many of the near-shore stations.



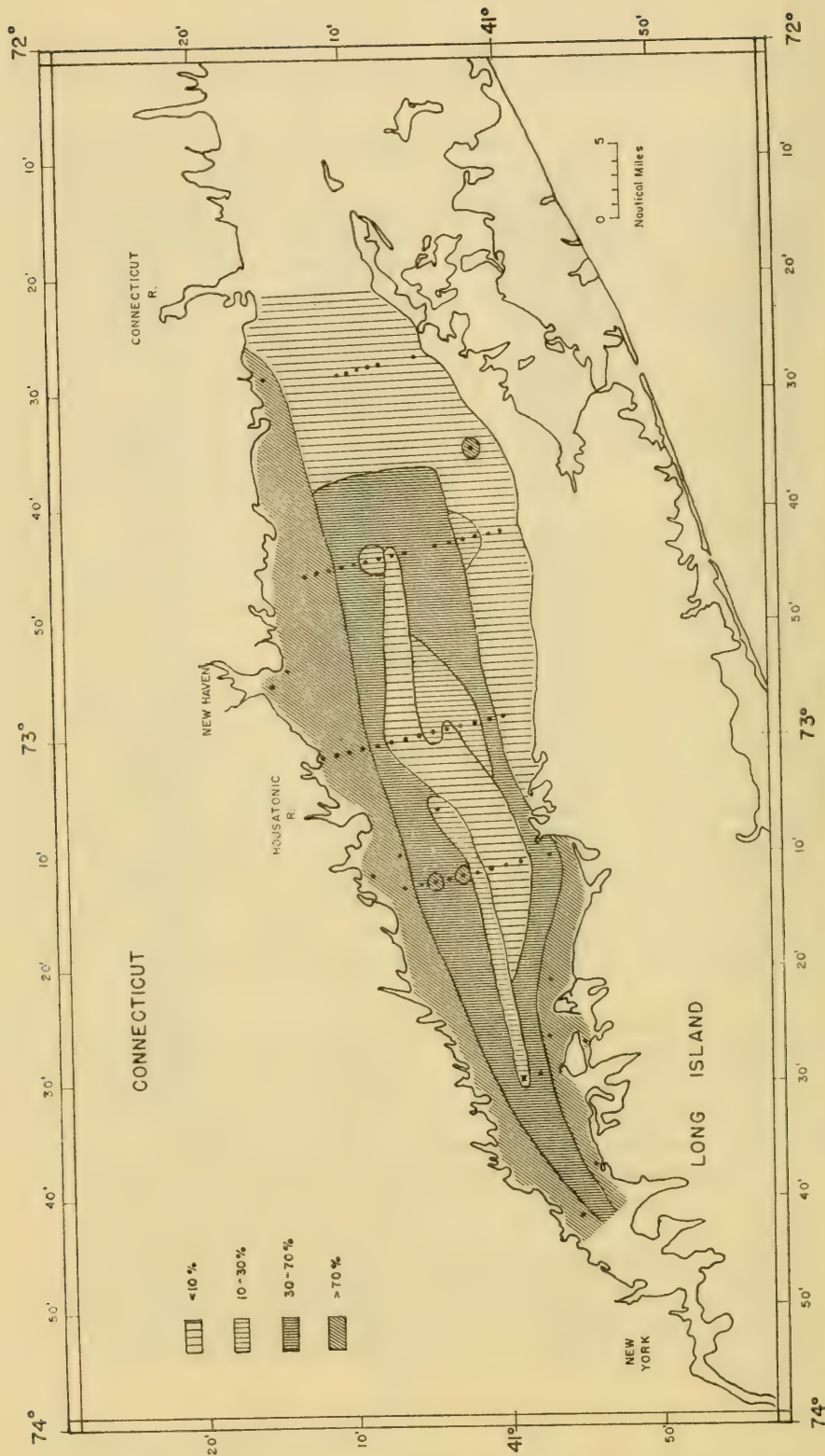


FIG. 5.—Areal distribution of *Elphidium clavatum* in percent of the living population.

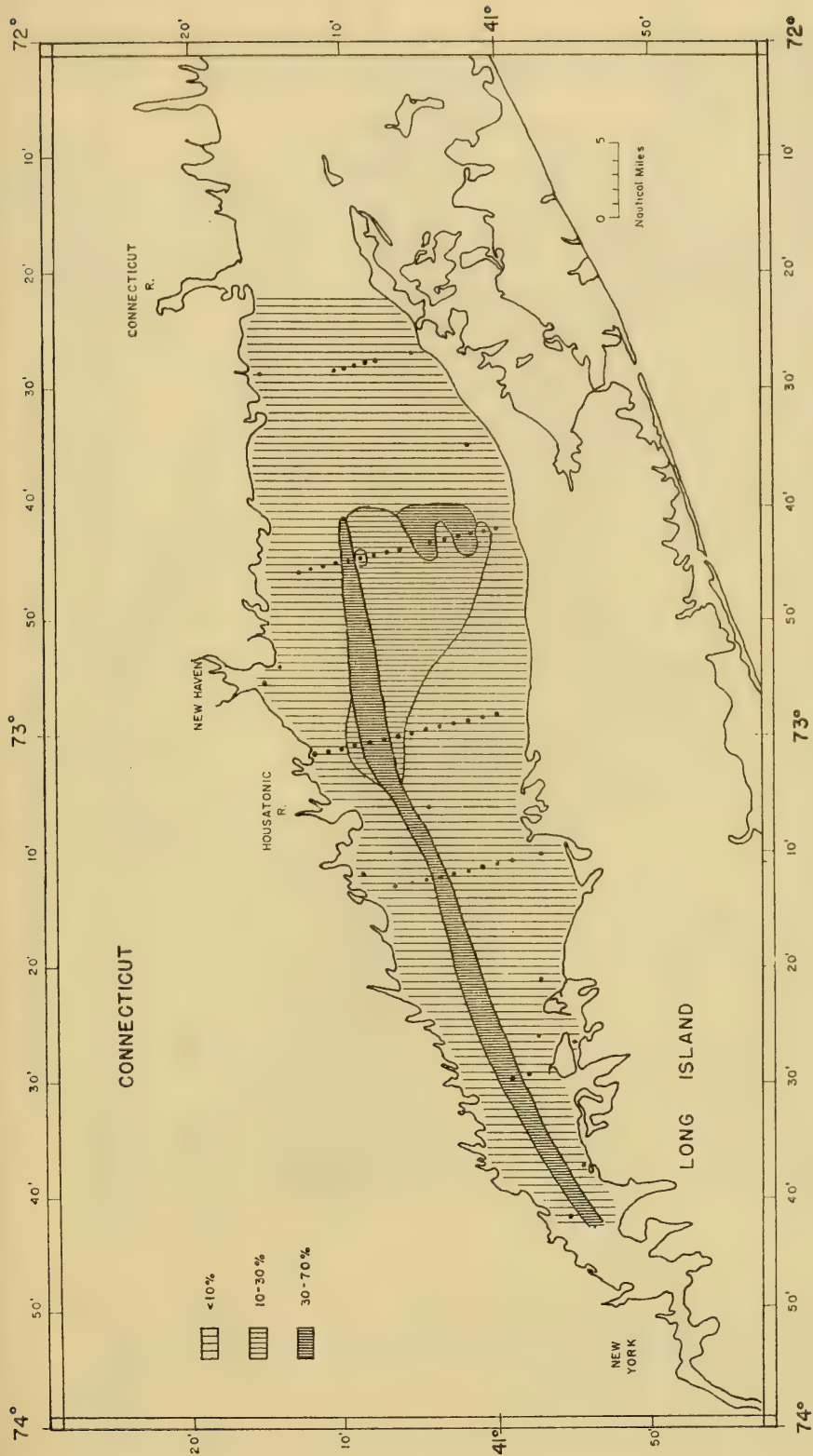


FIG. 6.—Areal distribution of *Buccella frigida* in percent of the living population.

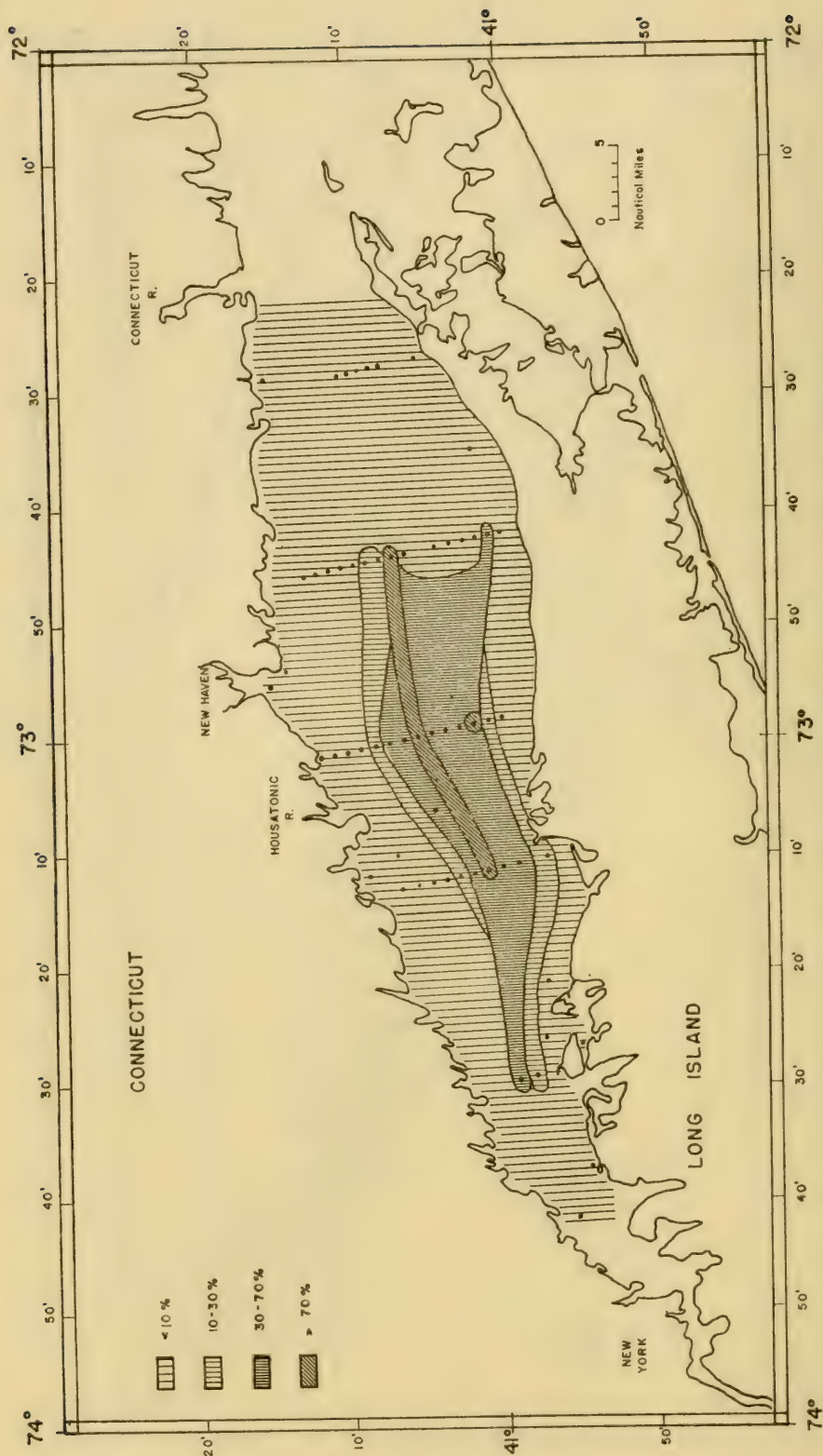


FIG. 7.—Areal distribution of *Eggerella advena* in percent of the living population.

## SIZE OF THE LIVING POPULATION

The actual number of living individuals per station for each of the abundant species was averaged for the depth ranges 0-10 m., 10-20 m., 20-30 m., and 30-40 m. The results are shown in figure 8. *Elphidium clavatum* averages over 300 living individuals at depths of less than 10 m. and over 100 at depths of 10-20 m. It averages less than 20 individuals at depths greater than 20 m. *Buccella frigida* shows a maximum in the range 10-40 m., whereas *Eggerella advena* is most abundant at depths of greater than 20 m. Figures 5-7 show that *E. clavatum* is relatively abundant at depths of less than about 20 m. and that *E. advena* is relatively abundant at greater depths. The histograms of figure 8, however, show that in terms of numbers of living individuals *E. clavatum* is by far the most abundant species, and therefore the greatest concentration of living individuals is in the near-shore areas.

Figure 9 shows the distribution of the living population in numbers of individuals per uniform sample. The numbers used for traverse 3 are averages from the seasonal stations. At depths of less than 15 m. the living population is usually over 200 individuals. The larger part of the central areas is in the range of 30-90 individuals per sample. At stations 8-11 in traverse 3 and stations 44 and 45 in traverse 4 the number of living individuals is in the range of 90-200. Occurrences of less than 30 individuals are most common along the north shore of Long Island east of longitude 73° and in traverse 5.

The standing crop of Foraminifera in L.I.S. is estimated to be 110 per sample. This figure was obtained by averaging the number of living Foraminifera in the top centimeter of the 88 seasonal samples of traverse 3. Because this average is based on many stations sampled seasonally, it is believed to be the best estimate attainable. At depths of 10-20 m. the average number of living Foraminifera in the seasonal stations of traverse 3 is 177, while at depths of greater than 20 m. it is 62. The shallowest station in the seasonal traverse is 10 m., and therefore to obtain an estimate of the living population in the 0-10-m. range, miscellaneous shallow-water stations were used. The area just north of Long Island east of longitude 73° was excluded. The average number of living Foraminifera at eight stations in the 0-10-m. range is 335.

## ZONATION OF THE LIVING POPULATION

Examination of the data indicates that the three most abundant species can be used to construct a foraminiferal zonation of L.I.S.



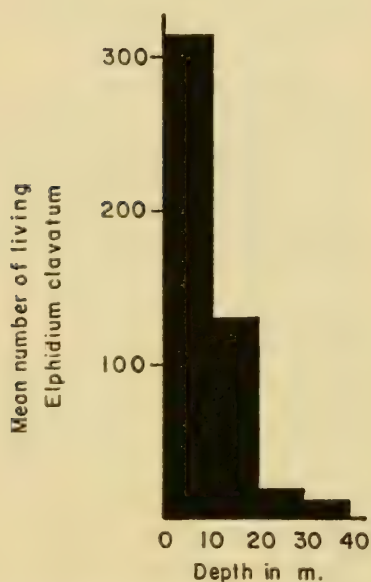
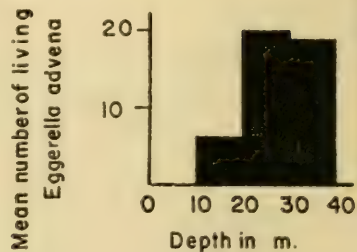
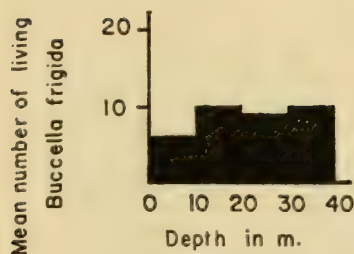


FIG. 8.—Distribution of abundant species with depth.

The exact limits of the zonation were chosen empirically through careful examination of table 3 (page 72). The following zones are recognized:

*Elphidium clavatum* zone:

*E. clavatum*  $\geq 60\%$

*B. frigida*  $< 9\%$

*Buccella frigida* zone:

*B. frigida*  $\geq 9\%$

*E. advena*  $< 19\%$

*Eggerella advena* zone:

*E. advena*  $\geq 19\%$

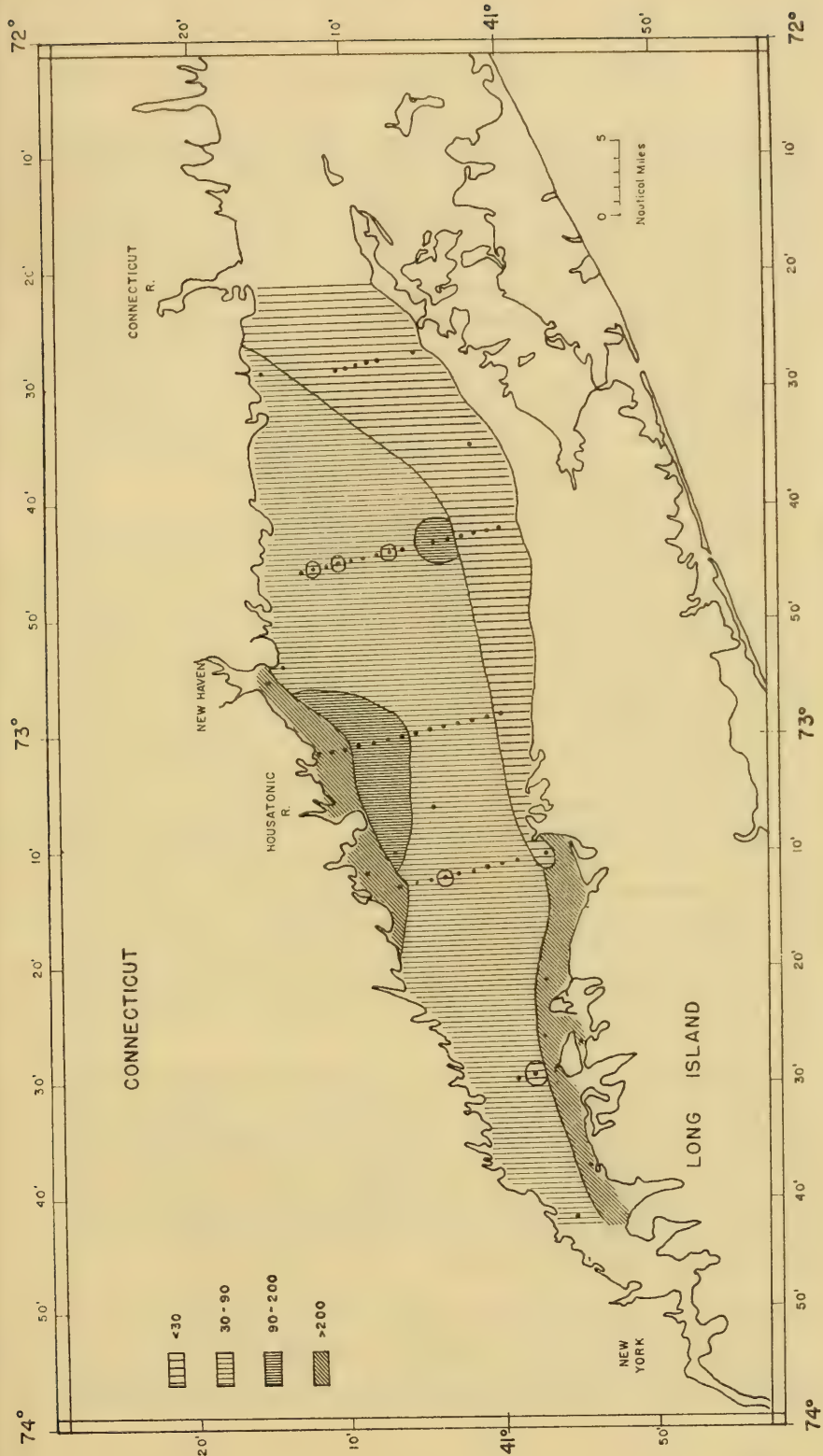


FIG. 9.—Areal distribution of living population in number of specimens per sample.

The percentage limits placed on the zones reflects the pattern which is repeated in the traverses. The limits are, of course, artificial, and in reality the transition from one zone to another is not sharp but gradational. Examination of table 3 indicates that if the percentages from any particular set of seasonal stations in traverse 3 is used, the exact location of a zone's boundary may vary. For instance in June of 1961 the boundary for the *E. clavatum* zone lies about 3 nautical miles off the Connecticut shore, whereas in November of 1962 the boundary lies 2 nautical miles off the Connecticut shore. Similarly, the exact limits of the *B. frigida* and *E. advena* zones also fluctuate. The pattern, however, is always repeated. Figure 10 shows the zonation of the living population in L.I.S. The percentages used for traverse 3 are from the grand stations.

*Elphidium clavatum* zone.—The percent of *E. clavatum* increases shoreward, and some of the stations less than a mile from shore are almost entirely composed of this species. *E. clavatum* is by far the most abundant species in this zone. The upper limit of *B. frigida* is fixed by definition at 8 percent. *E. advena* either occurs with very low frequencies or is absent altogether. *Elphidium pauciloculum*, *E. varium*, and *Reophax dentaliniformis* are commonly present, but usually make up less than 15 percent of the living population. The mean depth of stations in this zone is 12 m. and the range 3-23 m.

*Buccella frigida* zone.—This zone marks a transition between the *E. clavatum* and *E. advena* zones. At many of the stations in this zone *E. clavatum* and/or *E. advena* are more abundant than *B. frigida*. However, *B. frigida* is usually relatively more abundant in its zone than elsewhere. *Elphidium pauciloculum*, *E. varium*, *Fissurina laevigata*, and *Reophax dentaliniformis* commonly occur, but usually do not make up more than 15 percent of the living population. The mean depth of stations in this zone is 25 m. and the range 15-33 m.

*Eggerella advena* zone.—In this zone the living population is dominated by *E. advena*. Occasionally *E. clavatum* or *B. frigida* may be relatively more abundant than *E. advena*, but usually the reverse is true. *Elphidium pauciloculum*, *E. varium*, *Fissurina laevigata*, and *Reophax dentaliniformis* occur, but usually make up no more than 20 percent of the living population. The mean depth of stations in this zone is 29 m. and the range 16-39 m.

#### COMPARISON OF THE NUMBER OF LIVING INDIVIDUALS IN TRAVERSES 2 AND 3

Traverse 2 was sampled on November 19, 1962, and one of the sampling times of traverse 3 was on November 20, 1962. Owing

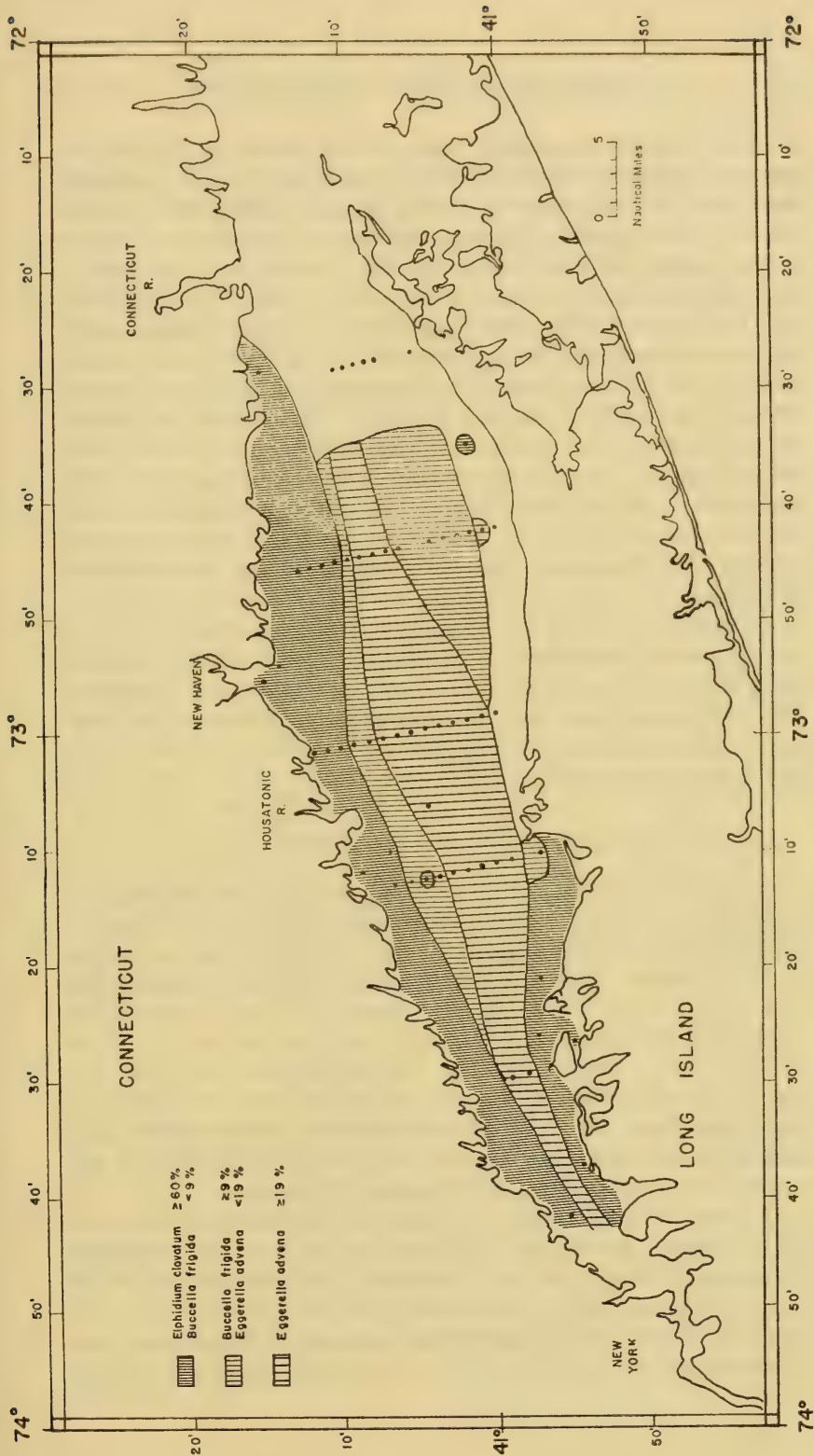


FIG. 10.—Zonation of living population.



to the proximity of sampling times, it was decided to compare the numbers of living individuals in the traverses. I have previously noted that binomial tests on paired samples indicate that samples from the offshore area (*Eggerella advena* zone) give the best estimate of the number of living individuals at a station. Five stations in traverse 2 and seven stations in traverse 3 were in the *E. advena* zone in November 1962. The distribution-free Wilcoxon two sample test was chosen to test for significant differences in the living populations of the two traverses. This statistic tests for location and is discussed at length by Bradley (1960). Under the null hypothesis the two samples (of five and seven stations respectively) come from the same population. The scores ( $m$ ) of one sample and ( $n$ ) of the other where ( $m \leq n$ ) are ranked, and the ranks of the smaller sample are summed ( $R_m$ ). The critical values of  $R_m$  are tabled by Owen (1962). The 95-percent level for a two-tailed test was considered significant.

A value of  $R_m = 45$  was obtained which is significant at the 95 percent level. There were, then, a significantly greater number of living individuals in the *E. advena* zone of traverse 2 in November 1962. No attempt was made to compare traverse 4 which was sampled in November 1961 because traverse 3 was not sampled at that time and so comparisons would be unwarranted.

#### COMPARISON OF THE STANDING CROP WITH OTHER AREAS

In the Gulf of Maine, Phleger (1952) estimated the standing crop as 30,000 per sq. m. He made this estimate by averaging the number of living individuals in the top centimeter of his cores and multiplying by 1,000 because the area of each sample is about one-thousandth of a square meter. In L.I.S. the number of living Foraminifera, estimated in the same way but from seasonal samples, is 110,000 per sq. m. Phleger used a different staining method, and this may account for some of the difference. The stations from which Phleger made his estimate were almost all from depths of over 100 m., and none of his stations were as shallow as the deepest station in this study. It is, therefore, difficult to compare the two areas.

At depths of less than 10 m. the living population has an average of 335 individuals per sample. This average is based on near-shore samples taken in August and November. The greatest number of living individuals (756) was found at station 112 at a depth of 14 m. This station is located at the entrance to Huntington Bay. In New Haven Harbor at station 19 two samples taken a week apart

in August 1961 had 417 and 681 living individuals respectively. Phleger (1956) has reported that in San Antonio Bay, Tex., the largest living populations are located near the entrance of the Guadalupe River, where two stations contained 2,579 and 302 specimens respectively. Lankford (1959) has found very large living populations in the deltaic marine environment of the Mississippi Delta. The average number of living individuals in this area was 2,500. Phleger has suggested that very large living populations near the entrance of river mouths are due to high production of organic matter in these areas. The largest rivers entering L.I.S. are the Housatonic and Connecticut Rivers. Unfortunately, none of the stations in this study is located near the entrances of these rivers. Riley (personal communication) has indicated that at the entrances of these rivers the concentration of phytoplankton is about the same as in other areas of the Sound. He suggested that the mortality of fresh-water phytoplankton as they enter marine waters might constitute an additional source of food. At any rate, the large living population in New Haven Harbor, which has several small rivers entering it, and at the entrance to the inside of Huntington Bay is consistent with similar observations in other areas.

Walton (1955) based his estimate of the standing crop in Todos Santos Bay, Calif., on seasonal samples. Most of his samples were from deeper water, but he has given averages for every 10 fathoms of depth in the 0-50-fathom range. His average living population per sample in the depth range of 10-20 fathoms is 66. The average living population in the comparable depth range of 20-40 m. in the present study is 62. In the 0-10-fathom range, however, Walton found less than 40 individuals per sample. In L.I.S. this depth range would have over 200 individuals per sample.

#### DISTRIBUTION OF THE TOTAL POPULATION

Figure 11 shows the distribution of the three most abundant species in percent of the total population for the 13 grand stations of traverse 3. The distributions are similar to those of the living population. However, the maxima of *Buccella frigida* and *Eggerella advena* are much less pronounced. *Elphidium clavatum* is still most abundant at the ends of the traverse, but it is relatively more abundant in the central area than it was in the living population. Figures 12 and 13 show the distributions at traverses 2 and 4 respectively.

The areal distribution of *Elphidium clavatum* in percent of the total population is shown in figure 14. The distribution pattern is

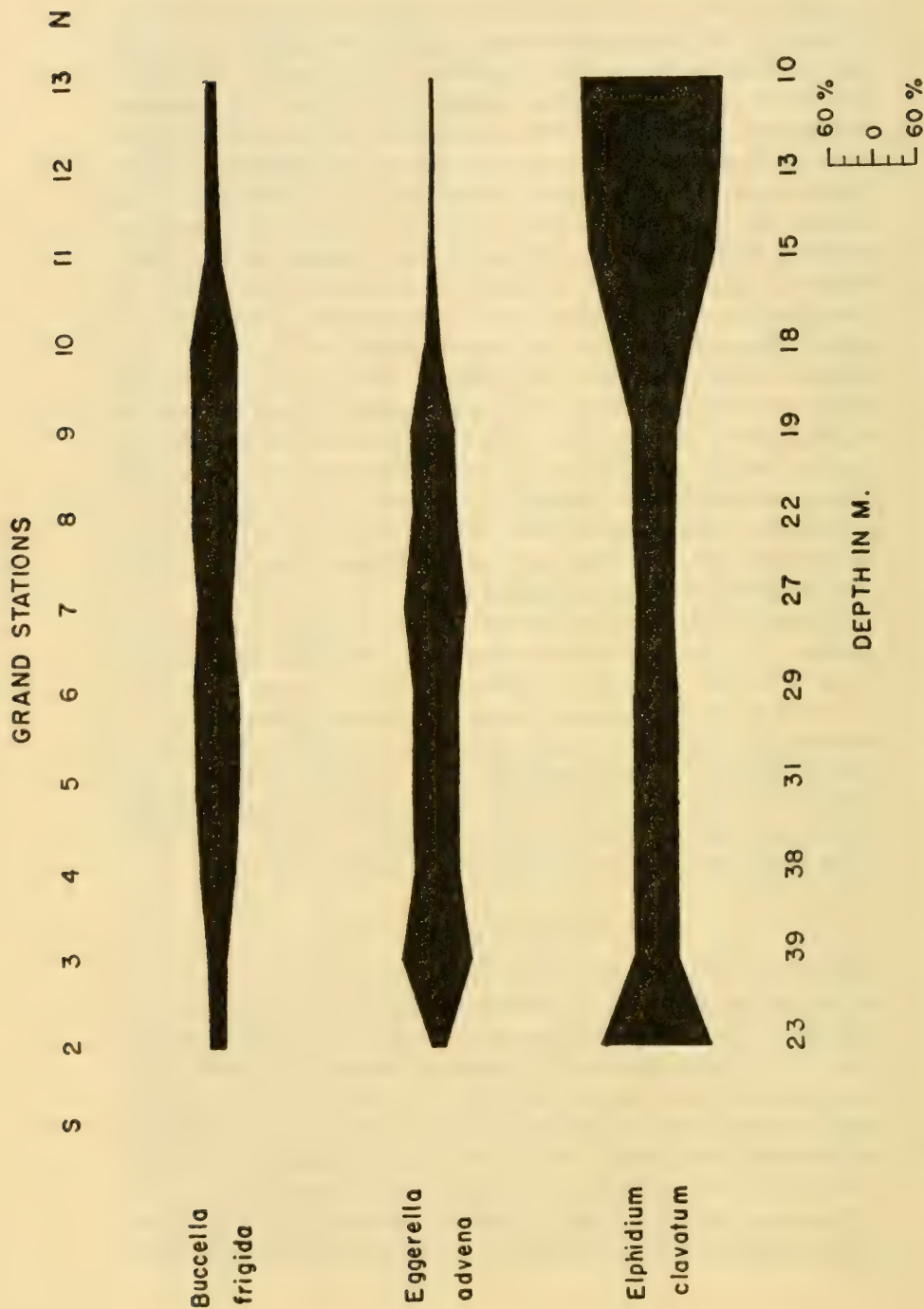


FIG. 11.—Distribution of abundant species in percent of the total population at grand stations of traverse 3.

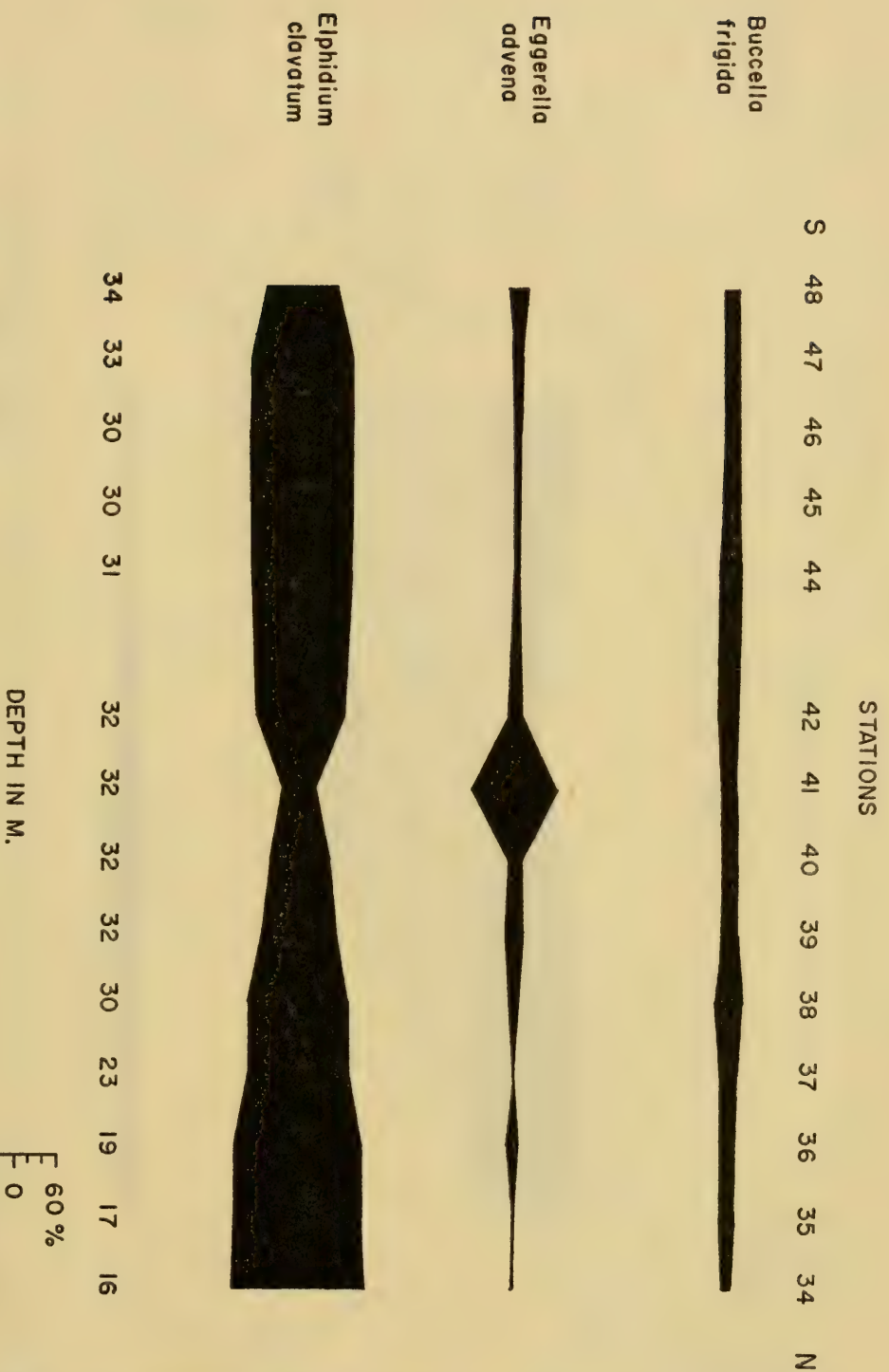


FIG. 13.—Distribution of abundant species in percent of the total population at stations of traverse 4.



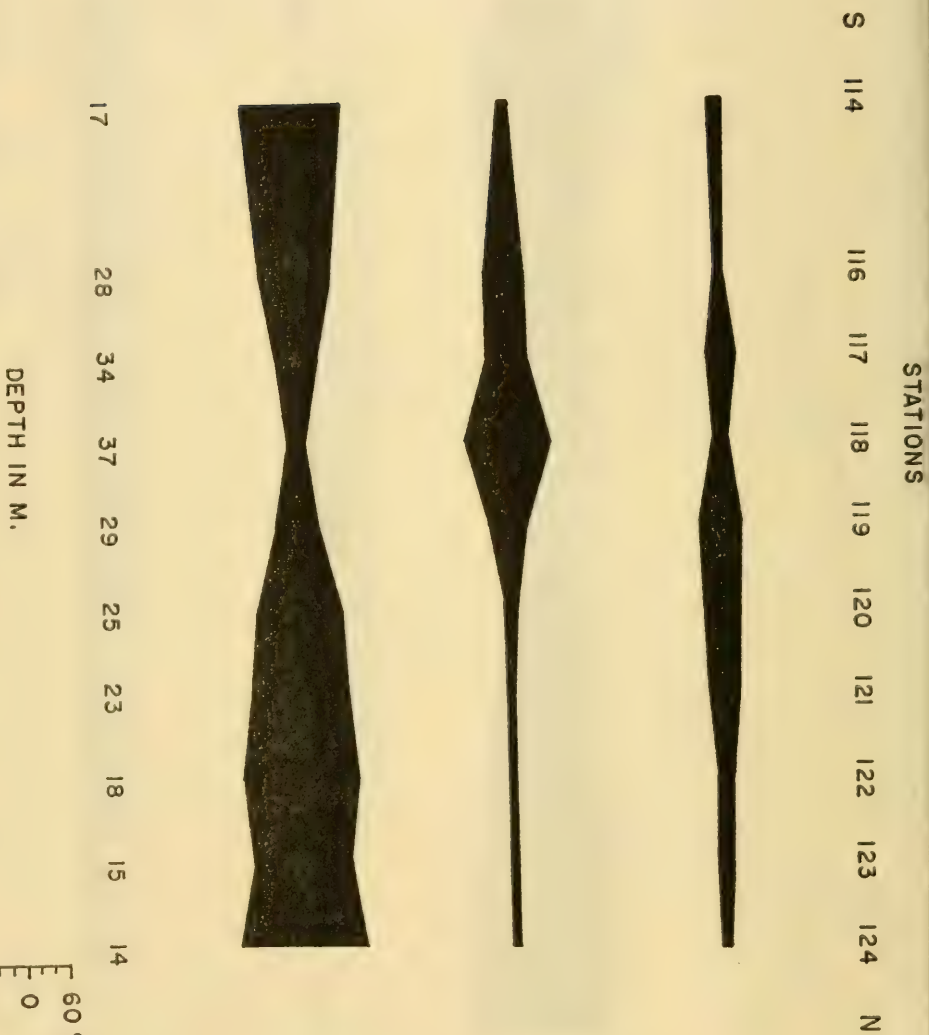


FIG. 12.—Distribution of abundant species in percent of the total population at stations of traverse 2.

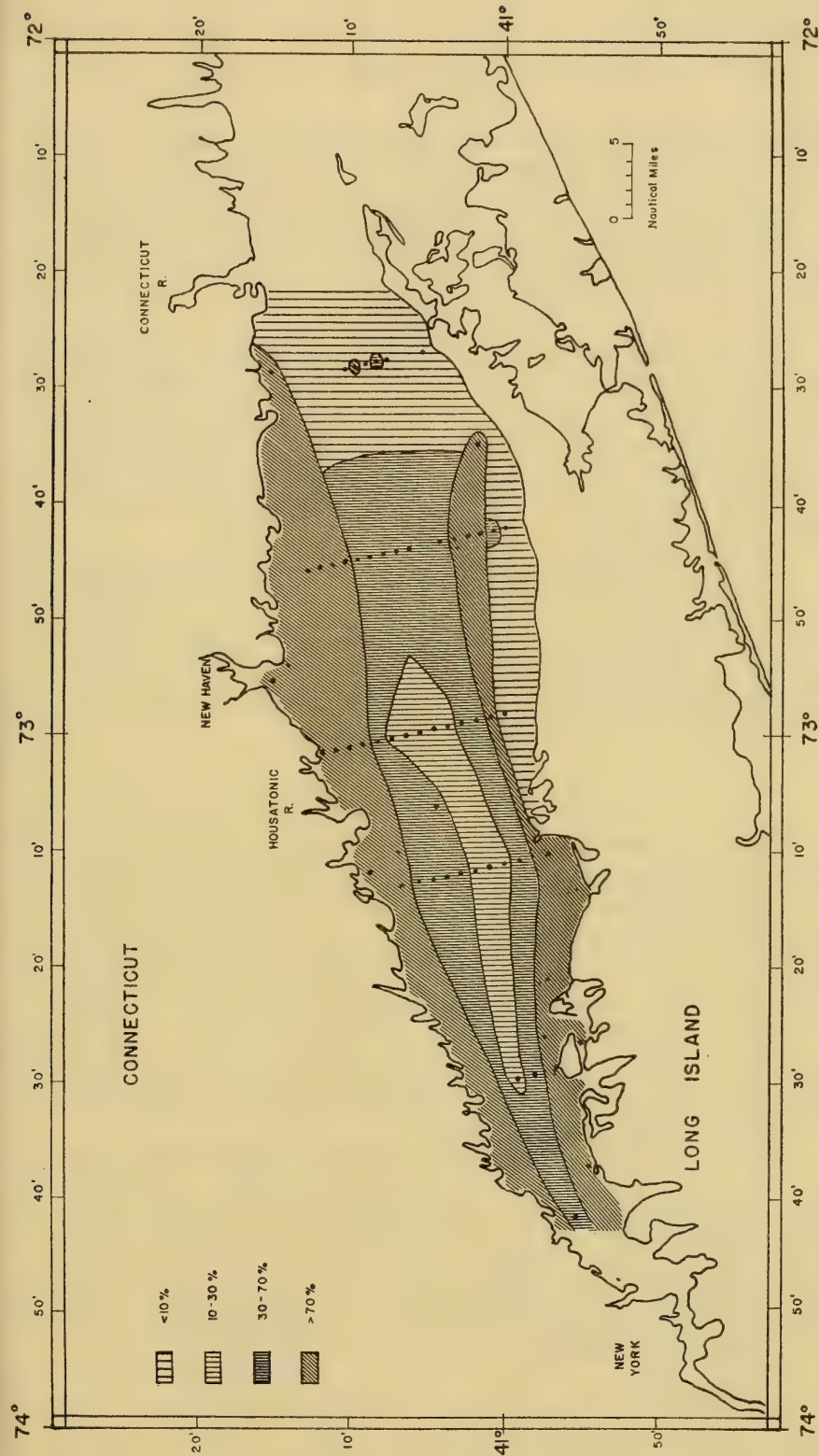


FIG. 14.—Areal distribution of *Elphidium clavatum* in percent of the total population.

quite similar to that of the living population shown in figure 5. The principal difference is that in percent of the total population *E. clavatum* is more abundant in all areas. The areas where *E. clavatum* comprises over 70 percent of the population have been extended for about another mile offshore, and even in the central areas of the Sound *E. clavatum* commonly occurs with a frequency of over 20 percent.

The areal distribution of *Buccella frigida* in percent of the total population is shown in figure 15. The distribution pattern of *B. frigida* is somewhat different from that previously noted. Instead of a narrow maximum-frequency band in the east which expanded to the west, we have a large area where *B. frigida* occurs with a frequency of 10-30 percent. There is, however, a general increase in frequency toward the central areas from a minimum along the shore.

The areal distribution of *Eggerella advena* in percent of the total population is shown in figure 16. This distribution of *E. advena* is not as symmetrical as it was in the living population. There is still a general increase toward the central areas, but the maximum frequency is only 63 percent instead of 92 percent, and in traverse 3 the area of maximum frequency is somewhat south of center.

#### SIZE OF THE TOTAL POPULATION

Figure 17 shows the distribution of the total population in numbers of specimens per uniform sample. The numbers used for traverse 3 are from the grand stations. The near-shore areas, with the exception of the north shore of Long Island east of longitude 73° and traverse 5, contain over 500 individuals per sample. An area of 200-500 individuals per sample occurs on the north side of traverses 2 and 3 and expands eastward to cover nearly the entire area of traverse 4. The western portion of the central area contains a large area of 90-200 individuals per sample which decreases in size eastward and is nearly absent in traverse 4.

The general pattern of the total population is similar to that of the living population. The near-shore areas contain the greatest numbers of individuals, whereas the offshore areas contain far fewer. The north shore of Long Island east of longitude 73° and traverse 5 is conspicuously barren in both cases. In general, the areas where the greatest number of empty tests occur are also the areas of maximum living Foraminifera.

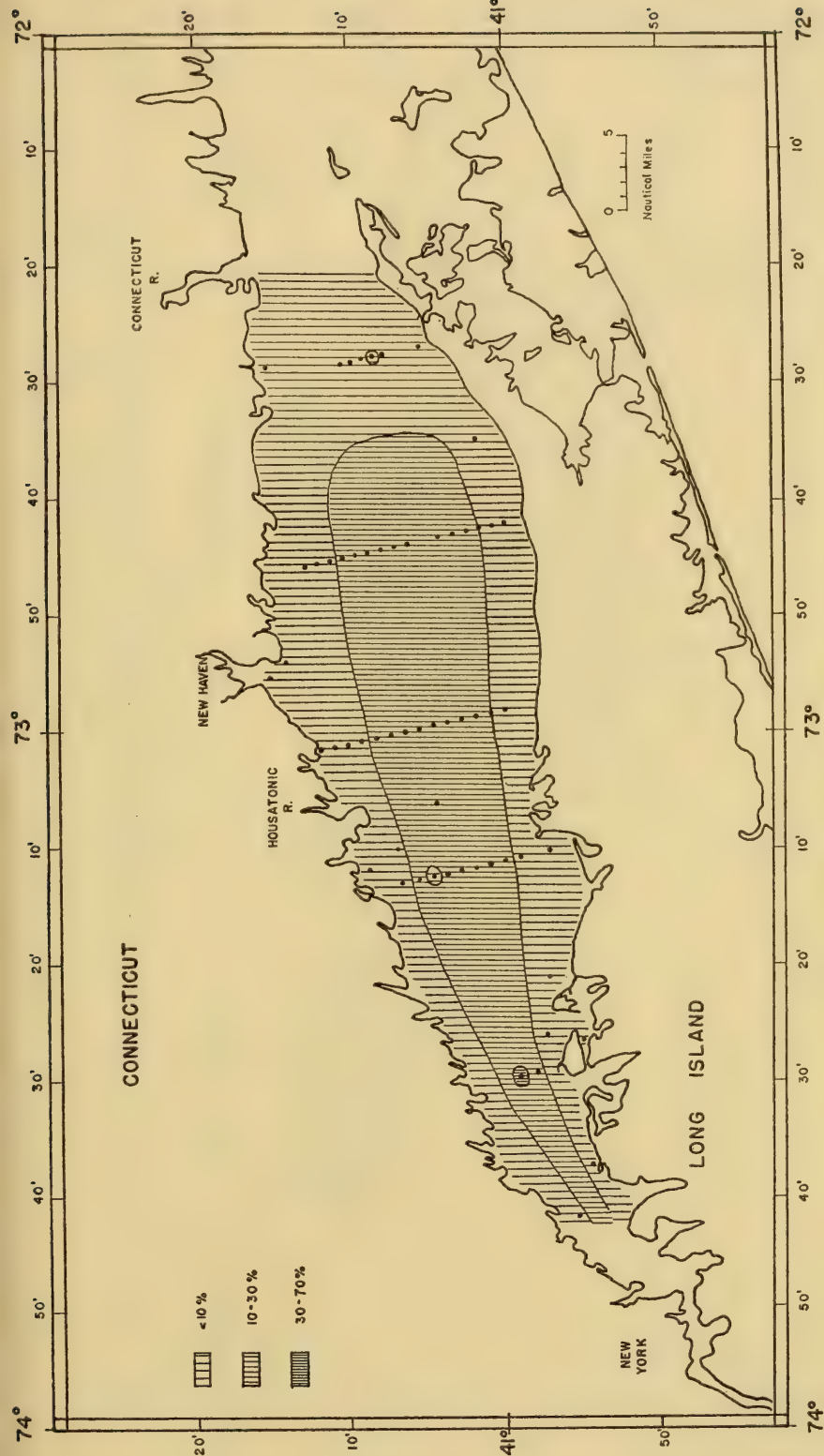


FIG. 15.—Areal distribution of *Buccella frigida* in percent of the total population.



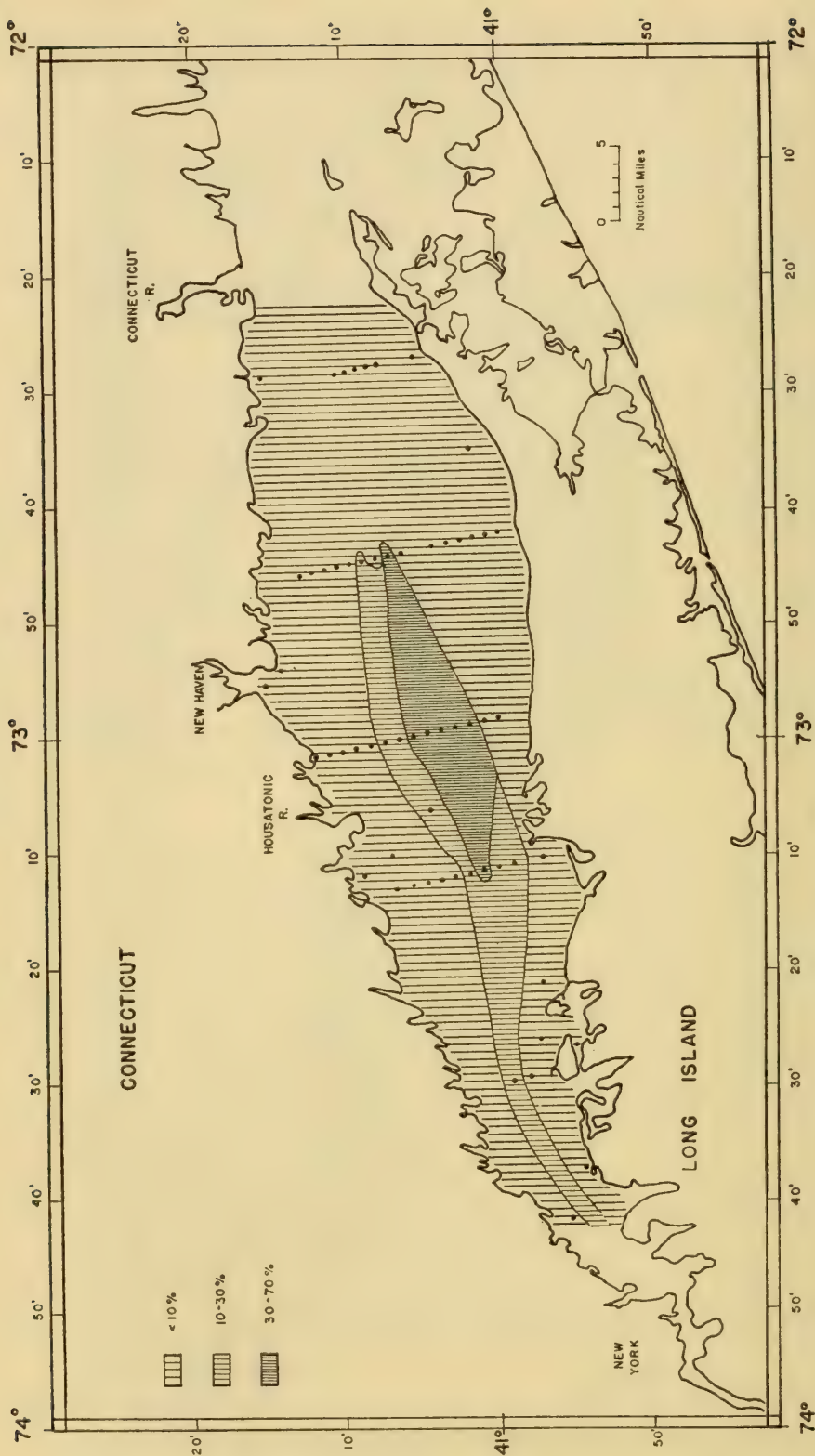


Fig. 16.—Areal distribution of *Eggerella advena* in percent of the total population.

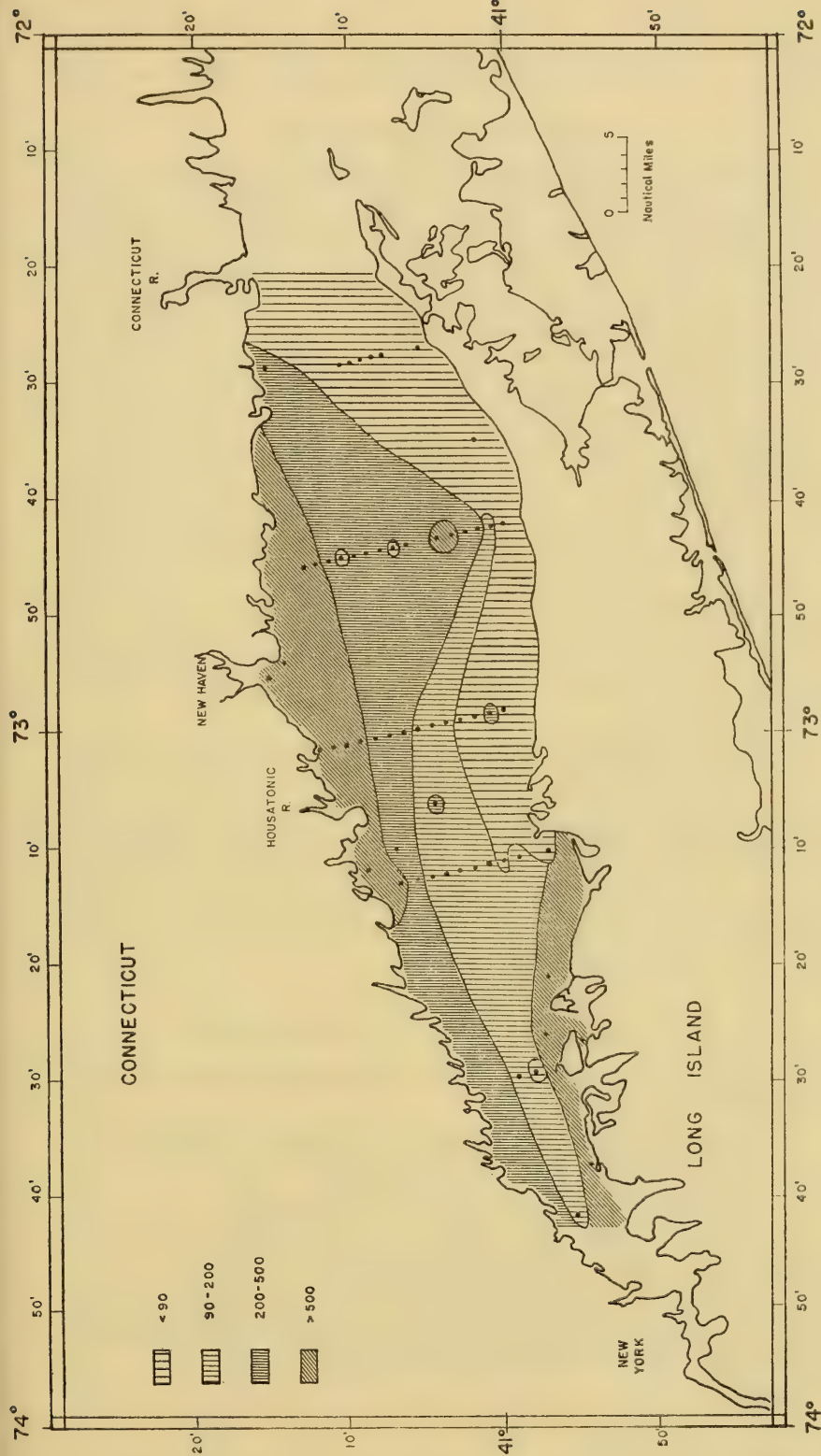


FIG. 17.—Areal distribution of total population in number of specimens per sample.

## ZONATION OF THE TOTAL POPULATION

Zonation of the total population using the same percent limits that were used for the living population is shown in figure 18. The *Buccella frigida* zone is now somewhat more extensive and the *Eggerella advena* zone correspondingly more compressed. This is due to the lower frequencies with which *E. advena* occurs in the total population. This species is usually represented by only a few dead individuals, so its percent in the total population depends heavily on the number of living individuals. In general, the agreement between the zonation of the living and total populations is quite good. The average depth of stations in the *E. clavatum* zone based on the total population is 11 m. and the range 3-19 m. Stations in the *B. frigida* zone based on the total population have an average depth of 26 m. and a range of 15-33 m. In the *E. advena* zone based on the total population the average depth of the stations is 30 m. and the range 19-39 m. The mean depth of stations in the *E. advena* and *B. frigida* zones is 1 m. deeper than it was in the zonation of the living population, whereas the mean depth of the *E. clavatum* zone is 1 m. shallower. The ranges are more restricted except in the case of the *B. frigida* zone, where it remained the same.

Figures 14-16 show that the distribution of the abundant species in the total population are comparable to their distributions in the living population (figs. 5-7). The major difference is that in the total population there is less accentuation of the species distribution, that is, *E. clavatum* and *B. frigida* are more evenly distributed in the deeper areas. It is likely that dead individuals of these species are transported into deeper areas, and so the total population in these areas has a higher percentage of them.

## SUMMARY OF THE DISTRIBUTION OF THE FORAMINIFERA

In summary the distribution of the Foraminifera has the following characteristics:

1. The fauna is composed of 23 species belonging to 15 genera.
2. No planktonic Foraminifera were found.
3. The number of species increases from west to east.
4. *Reophax dentaliniformis* and *R. nana* are common in L.I.S. but are not found in adjacent open ocean waters.
5. The species *Elphidium clavatum*, *E. pauciloculum*, *E. varium*, *Buccella frigida*, and *Eggerella advena* make up about 90 percent of the total as well as of the living population.

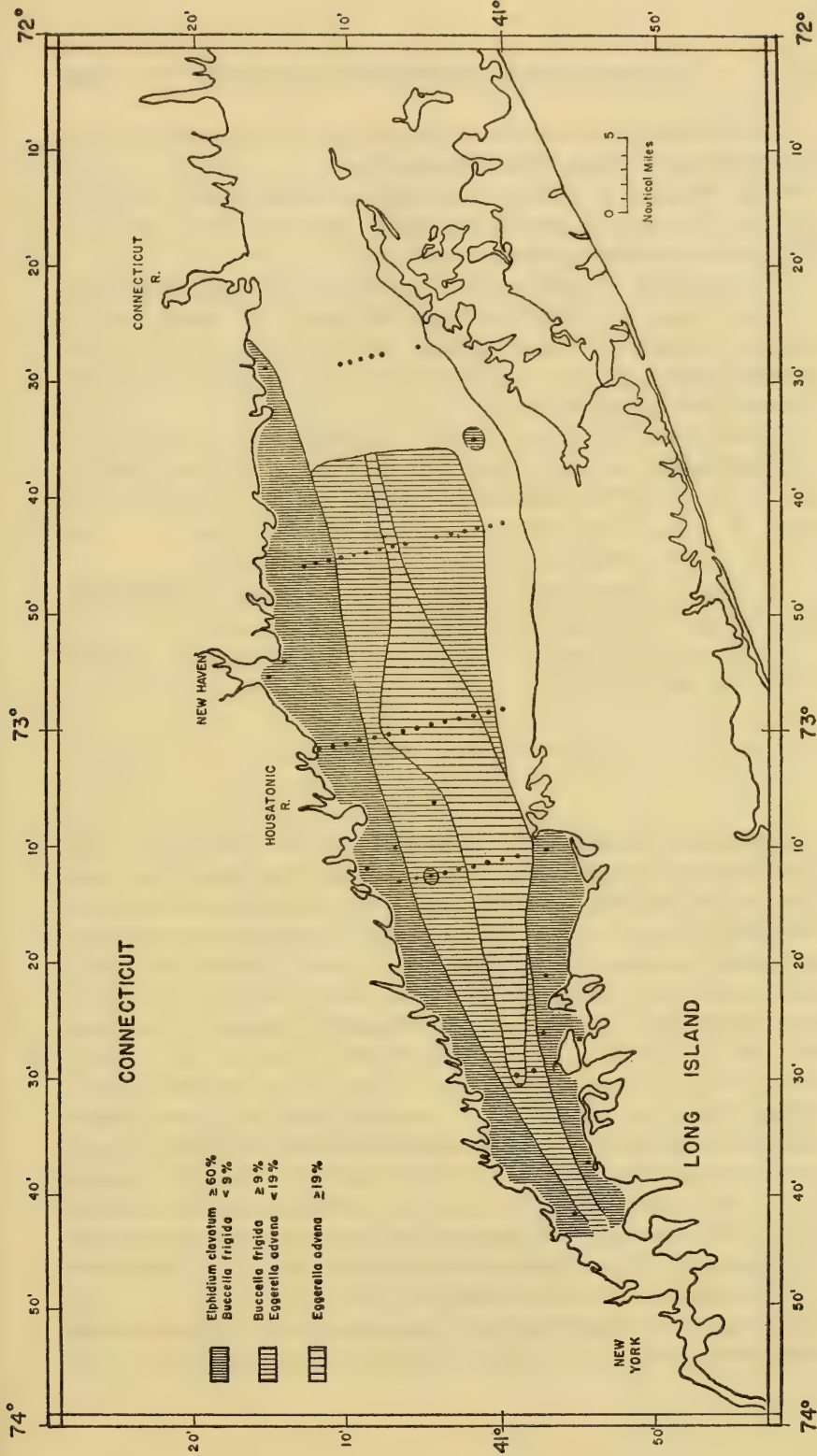


Fig. 18.—Zonation of total population.



6. Of these *E. clavatum*, *B. frigida*, and *E. advena* are most abundant and usually comprise over 75 percent.

7. *E. clavatum* is most abundant in near-shore areas ( $<20$  m.), whereas *E. advena* is most abundant in offshore areas ( $>20$  m.). *B. frigida* is abundant at depths of 10-40 m.

8. These three abundant species can be used to construct a foraminiferal zonation of L.I.S. In the living population the mean depth of stations in the *Elphidium clavatum*, *Buccella frigida*, and *Eggerella advena* zones is 12 m., 25 m., and 29 m. respectively. The depth ranges of these zones overlap.

9. The size of the living population based on seasonal samples is 110 individuals per sample. At depths of 10-20 m. the living population averages 177 individuals per sample, while in the 20-40-m. range it averages 62. Miscellaneous shallow-water stations in the 0-10-m. range average 335 living individuals per sample.

10. The *E. advena* zone of traverse 2 contained a significantly greater number of living individuals than did traverse 3.

11. The distribution of the total population closely approximates that of the living population.

## SEASONAL SAMPLES

### INTRODUCTION

Traverse 3 was sampled seven times during the period June 1961 to November 1962 for the purpose of establishing whether or not there is any seasonal variation in the living population. To do so, the samples must be shown to be a reliable estimate of the number of living Foraminifera at a given time. Table 2 shows that in the near-shore areas ( $<20$  m.) only two of the five sample pairs tested have numbers of living individuals that can be considered to be from the same distribution. In the offshore area ( $>20$  m.) five of the seven sample pairs tested indicate they are from the same distribution. The offshore area, then, is more likely to give a better estimate of the actual number of living individuals at a station. However, in the offshore area it is impossible to sample at exactly the same location each time the traverse is sampled. Consequently, it is desirable to treat the entire offshore area of traverse 3 as a single unit or population. At any given time a sample of the living population will be composed of several subsamples (stations).

In order to test the reliability of this assumption, it was decided to compare stations in the *Eggerella advena* zone at a given time. Five

of the ten stations in this zone on the traverse of March 1962 were chosen at random for comparison with the remaining five. The ten stations in the *E. advena* zone on the traverse of June 1962 were subdivided in the same way. The next step was to test whether two samples (five stations each) taken at the same time came from the same population. The test statistic chosen was the distribution-free Wilcoxon two sample test which was discussed earlier.

Table 5 (page 80) shows the results of the Wilcoxon test on the total living population and the living populations of *Elphidium clavatum*, *Buccella frigida*, and *Eggerella advena* for the traverses of March 1962 and June 1962. No significant  $R_m$  value was obtained, indicating that the two samples for March 1962 and the two samples for June 1962 are from respective identical populations.

#### SEASONAL VARIATIONS IN THE LIVING POPULATION

*Eggerella advena* is the most abundant species in the *E. advena* zone and therefore it was the most rigorously tested. The stations in the *E. advena* zone at each sampling time are considered a sample and the Wilcoxon two sample test was made on all the possible 21 pairs from the seven sampling times. The results are shown in table 6 (page 81). Frequency distributions for the mean number of total individuals and the mean numbers of living *Elphidium clavatum*, *Buccella frigida*, and *Eggerella advena* in the *E. advena* zone at the seven sampling times are shown in figure 19. The number of living *E. advena* in October 1961 was significantly greater than at any other time with the exception of January 1962. During the winter of 1962 the number of living *E. advena* declined, and then in June 1962 there was a small maximum after which they declined to the significantly lower levels of September and November 1962. The early autumn maximum so pronounced in October 1961 was not observed in 1962.

The frequency distribution of *Elphidium clavatum* in the *E. advena* zone shows a maximum in June 1962. Table 7 (page 81) shows that June 1962 was significantly greater than September, November, and March, 1962. No significant difference was found between November and January 1962.

The frequency distribution of *Buccella frigida* in the *E. advena* zone has maxima in June 1961 and June 1962. Table 8 (page 82) shows that June 1962 was significantly greater than September and November 1962. None of the other pairs tested gave a significant value. Examination of the stations of June 1961 indicates that the

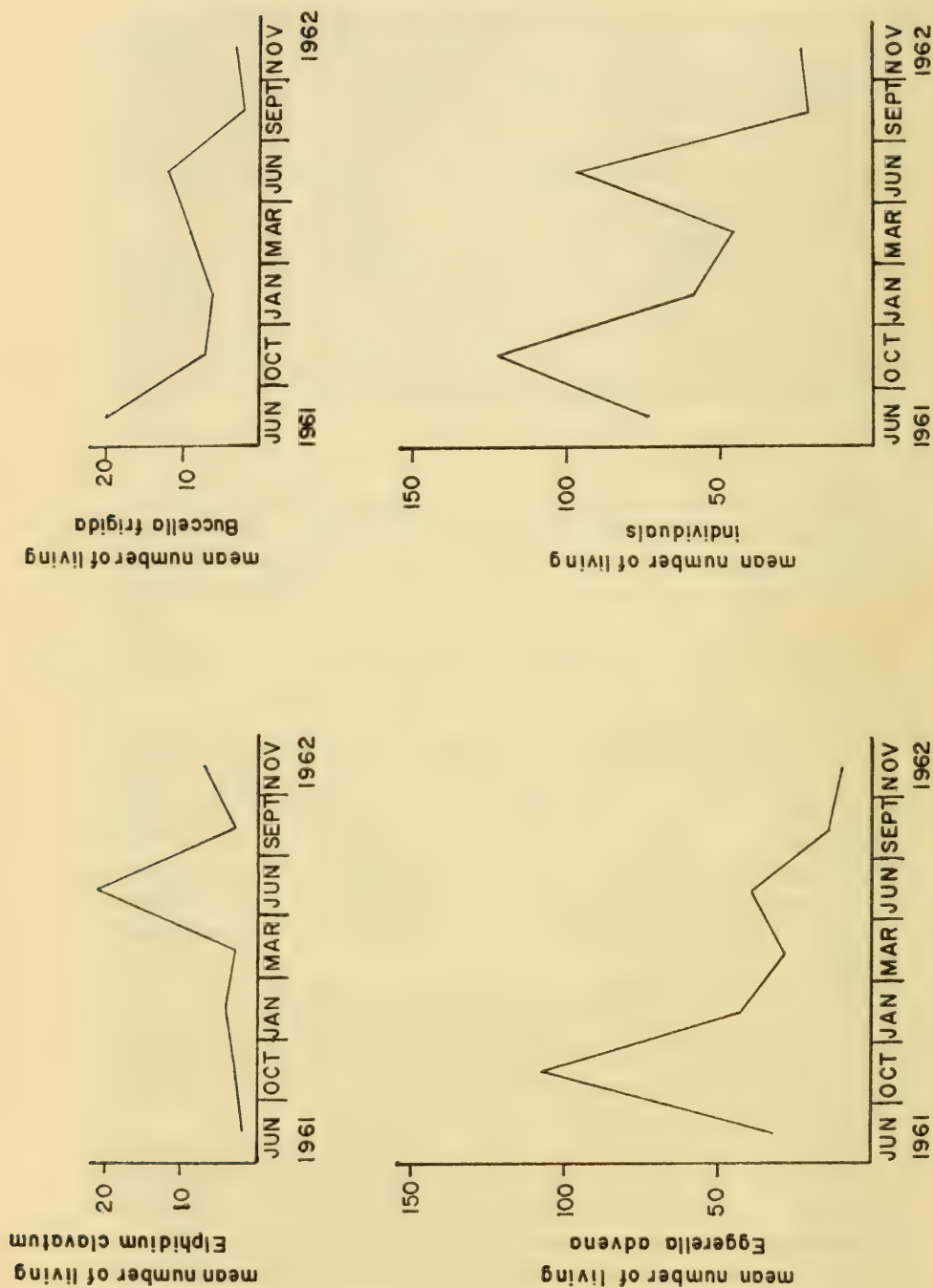


FIG. 19.—Seasonal distribution of living Foraminifera in the *Eggerella advena* zone.

high mean obtained for *B. frigida* at this time is misleading. Although 127 individuals were found at one station, the others contained comparatively few. Because the Wilcoxon test uses ranked sums, it is not sensitive to extreme values, and therefore June 1961 was not found to be significantly greater than any other time.

The frequency distribution of the total living population is similar to that of *E. advena*, the most abundant species in this zone. The June 1962 maximum, however, is accentuated owing to the abundance of *E. clavatum* and *B. frigida* at this time. Table 9 (page 82) shows the results of the Wilcoxon test performed on the total living population in the *E. advena* zone. October 1961 was not found to be significantly greater than June 1961. October 1961 was found to be significantly greater than January 1962, but not June 1962. June 1962 in turn was significantly greater than March and September 1962, but not January 1962.

Although the frequency distributions show times of maximum foraminiferal production, they do not indicate whether or not reproduction is occurring at all times of the year. Live megalospheric juveniles of *E. clavatum* with three or four chambers are easily recognizable and were counted during the period January 1962 to November 1962. The juveniles of this species are most abundant in the near-shore area, but because the variability of the actual number of individuals in a given sample in this area is great, the data are not treated quantitatively. Juveniles of *E. clavatum* are present throughout the year, and in the *E. advena* zone (as well as in the near-shore areas) the greatest number of juveniles was observed in June 1962. It is therefore likely that *E. clavatum* is reproducing all year long and only the rate of reproduction varies.

#### SIGNIFICANCE OF SEASONAL SAMPLES

In L.I.S. there was a significant increase in the number of living individuals in October 1961 and June 1962. The June maximum was due to an increase of all species, whereas the October maximum was due to an increase of *Elgerella advena*. In the water of Plymouth, England, Myers (1943) found that *Elphidium crispum* began gametogenesis in March and April right after the midwinter phytoplankton flowering. He reasoned that the increase in nutrients and light which precede a flowering are also beneficial to the benthonic microflora upon which *E. crispum* principally feeds, and therefore the phytoplankton cycle is a reliable index for the productivity of the microflora in general. Walton (1955) found maximum populations of



living Foraminifera in June and August in Todos Santos Bay, Calif., and he believed that these maxima were in response to the abundance of phytoplankton in late spring and summer. Parker and Athearn (1959) found the largest living population in Poponneset Bay, Mass., in June and suggested that this maximum might be related to maximum temperature because Myers (1935) and Bradshaw (1955) have shown that some species of foraminifers increase reproduction rates at higher temperatures.

Riley (1959) has shown that although there is a 20-fold variation in chlorophyll, the amount of organic matter in surface waters of L.I.S. varies within narrow limits. If the Foraminifera are indiscriminate feeders, and depend either directly or indirectly on organic matter in the water column, then the amount of food available is the same throughout the year. On the other hand if they depend on the phytoplankton either directly or indirectly, then their food will vary seasonally.

In L.I.S. the phytoplankton have a large midwinter flowering in February and March, several irregular summer flowerings, and in some years a large autumn flowering. The zooplankton have maxima in late spring and late summer. The Foraminifera were not abundant in March, and the next sampling time was in June. Therefore, if a late-spring increase had occurred it would not have been detected. Likewise, no samples were taken in July and August, and so it is not known whether or not the Foraminifera maintained their June maximum throughout the summer. In October 1961 *Eggerella advena* had a significant maximum, whereas none occurred in early autumn 1962. No data are available concerning possible phytoplankton flowerings during the autumns of 1961 and 1962.

The maximum temperature in L.I.S. occurs in August and the minimum in January or February. The temperature in June and October is about 16-18°C, the former being one month prior to the maximum and the latter one month after it.

The seasonal maxima obtained in this study are based on sampling times which are widely spaced. It may be said that the abundance of Foraminifera in October 1961 and June 1962 correlates in a general way with times of maximum temperature and with the increase of zooplankton in late summer and late spring, which in turn is correlated with the phytoplankton cycle. Until information regarding the feeding habits and importance of temperature for the species in question are available, these variables cannot be evaluated.

## SUMMARY OF SEASONAL SAMPLES

In summary, the frequency distributions and statistical tests indicate the following seasonal characteristics for the living population in the *Eggerella advena* zone:

1. The total number of living individuals was significantly greater in June 1962 than in March, September, or November, 1962.
2. *Elphidium clavatum*, *Buccella frigida*, and *Eggerella advena* showed a significant maximum in June 1962.
3. *Eggerella advena* was most abundant in October 1961 but did not show any maximum in early autumn of 1962.
4. Juveniles of *Elphidium clavatum* are present throughout the year, and it is likely that only the rate of reproduction varies.
5. The abundance of living Foraminifera in October and June correlates in a general way with the zooplankton and phytoplankton cycles in L.I.S. and with times of maximum temperature.

## THE FORAMINIFERA IN RELATION TO THE SEDIMENTS

## FORAMINIFERA IN SHORT CORES

Cushman (1948, p. 8) stated that benthonic Foraminifera live on the surface of muds and oozes or attached to objects on the bottom. Myers (1942) reported that *Elphidium crispum* could not extricate itself from the sediment if buried to a depth of 5-8 times its diameter. The benthonic Foraminifera have always been considered as epifaunal organisms.

In the present study samples were taken every centimeter to a depth of 4 centimeters in cores from five stations. Table 10 (page 83) shows the number of individuals in each species for the living and total populations. The suffix a indicates the sample is from the second centimeter, b the third centimeter, and c the fourth centimeter. The total population in the samples from any core is remarkably consistent. There appears to be little difference between the first and second centimeters in the cores, and at stations 74 and 107 there are actually more living individuals in the second centimeter. There is a trend toward fewer living individuals in the third and fourth centimeters of the cores.

The soft muds of L.I.S. contain a large number of molluscs and polychetes. The sediment is being continually turned over by the activities of these animals. In order for a foraminifer to remain on the surface, it would have to spend a considerable amount of its time climbing. Myers (1942) has shown that *Elphidium crispum* is

dormant during the winter and therefore would not offer any resistance to burial. Station 74 was sampled in March 1962 and stations 101-109 were sampled in September 1962. If the Foraminifera were dormant during this period then they certainly would be expected to become buried by the activities of the worms. On the other hand, even if they were active, it is likely that they would become buried by the activities of relatively much larger animals. If the benthonic Foraminifera in L.I.S. are truly epifaunal, then only these Foraminifera would survive and reproduce that were fortunate enough to remain on or be brought back to the surface. The alternative possibility is that the Foraminifera in L.I.S. are infaunal rather than epifaunal animals. Actually the sediment-water interface is not a sharp boundary in the soft muds of L.I.S. and so the terms epifaunal vs. infaunal at the interface are inexact. However, it must be remembered that living foraminifers were found 4 centimeters down in the cores.

Cytological investigations on a seasonal basis must be carried out in order to find out whether or not the foraminifers beneath the surface are feeding and reproducing. Since such investigations are beyond the scope of the present study, the answer must await further research.

#### PARTICLE-SIZE ANALYSES

Particle-size analyses were made on 59 samples using the standard methods of analysis described by Krumbein and Pettijohn (1938). The phi notation of Krumbein (1934) was used for the class limits where  $\phi = -\log_2$  of the diameter in millimeters. The results of each analysis were plotted on probability paper, and four of the statistical measures described by Inman (1952) were tabulated. These measures are: The phi median diameter ( $Md\phi$ ), phi mean diameter ( $M\phi$ ), phi deviation ( $\sigma\phi$ ), and phi skewness ( $\alpha\phi$ ). They are defined as follows:

$$\begin{aligned} Md\phi &= \phi_{50} \\ M\phi &= \frac{1}{2}(\phi_{16} + \phi_{84}) \\ \sigma\phi &= \frac{1}{2}(\phi_{84} - \phi_{16}) \\ \alpha\phi &= \frac{M\phi - Md\phi}{\sigma\phi} \end{aligned}$$

where  $\phi_{50}$ ,  $\phi_{84}$ , and  $\phi_{16}$  are percentiles. Table 11 (page 84) shows the results of the analyses. The letter *a* after each station number indicates that the second centimeter of core was used for the analysis. Stations 98, 56, 57, and 58 are exceptions.



Several different approaches were used in attempting to draw a generalized sediment map. One consisted of classifying the sediments by their  $Md\phi$  into sand, silt, or clay. The result was a map so overgeneralized that it was useless. The percent of sand, silt, and clay at each station was plotted on a triangular diagram in hope of obtaining discrete groups. The plots showed only two major groups with a transitional boundary. Plots of  $Md\phi$  vs.  $\sigma\phi$ , and  $Md\phi$  vs.  $\alpha\phi$  also lacked more than two clearly discrete mappable units. The classification of Niggli (1935), adapted to the Wentworth size classes by Pettijohn (1957) and modified by Dunbar and Rodgers (1957), which utilizes the first and third quartiles was finally adopted because it divides the sediment types into objective, manageable (six categories for L.I.S. sediments), and mappable units. The right-hand side of table 11 shows the sediments classified according to Niggli's scheme.

Examination of figure 20 shows that nearly the entire central area of L.I.S. is composed of clayey silt and silty sands. In traverses 2 and 3 more than half of the stations are composed of clayey silt. The sediment in these traverses changes to silty sand as Long Island is approached. Stratford shoal which is a topographic high in the center of the Sound midway between traverses 2 and 3 is composed of pebble sand. Farther east in traverse 4 silty sand is the dominant sediment. The area of silt shown between traverses 3 and 4 is probably of no significance because examination of table 11 shows that with the exception of station 34, the stations in traverse 4 classified as silt differ little from the stations called silty sand. Likewise, station 10 in traverse 3 differs little from stations 9 and 11 which are classified as clayey silts. The northern coast of Long Island east of longitude  $73^\circ$  is composed of coarse sand. Traverse 5 shows that the area of sand increases as the Sound narrows at its eastern end, and the silty sands become restricted into a narrow band. West of longitude  $73^\circ$  the northern coast of Long Island is irregular and the area of clayey silt shown on the map might have been anticipated from the shoreline configuration. Very little information is available for most of the near-shore areas, but the work of Ellis (1962) shows that the distribution of near-shore sediments is complex.

Examination of table 11 indicates that most of the sediments are poorly sorted. The silty sands have an average  $\sigma\phi$  of 2.3; the clayey silts, 2.8. Most of the silty sands are skewed toward the fines, whereas the clayey silts are skewed toward the coarser sizes. The sands are, in general, better sorted and have an average  $\sigma\phi$  of 1.5.



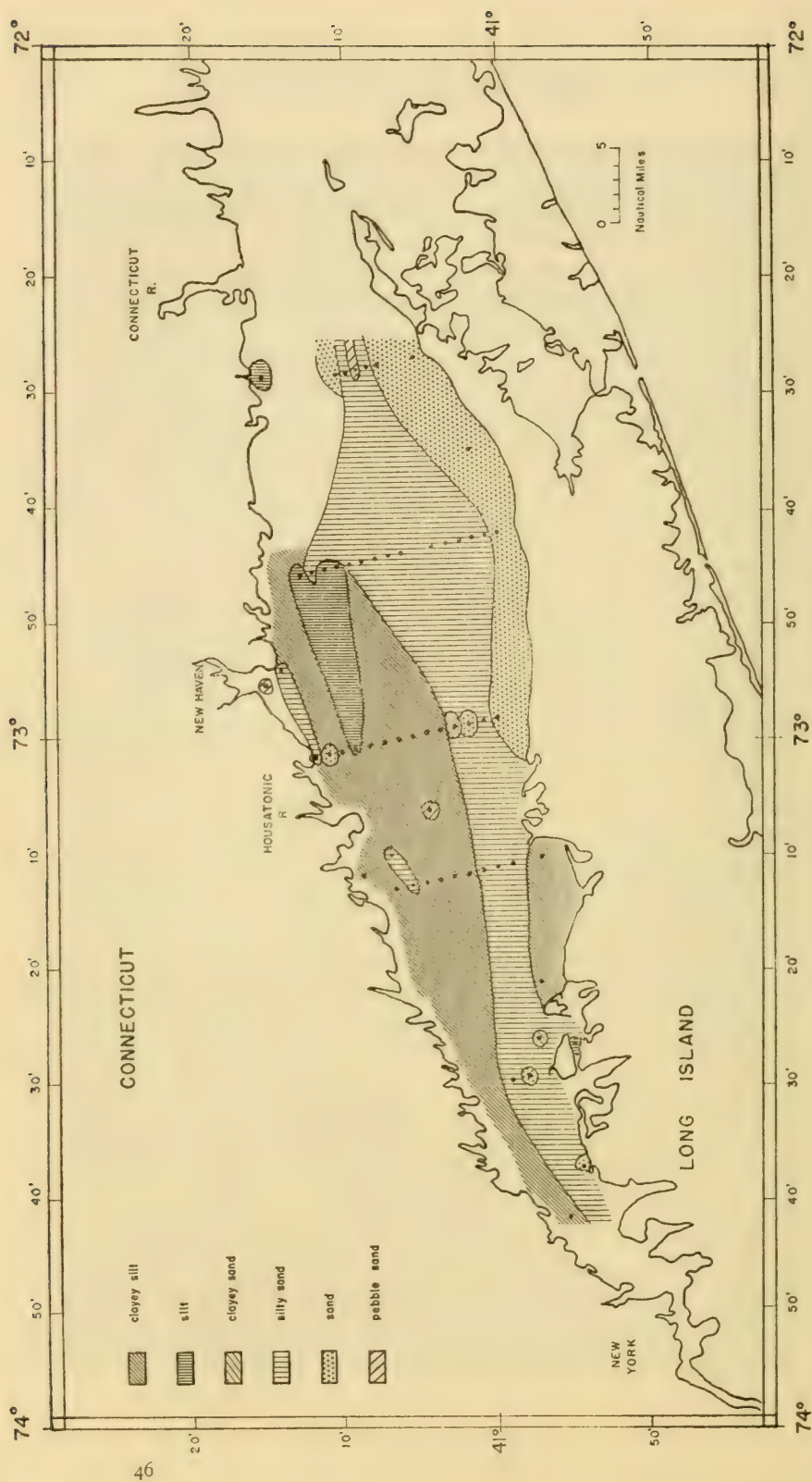


FIG. 20.—Areal distribution of sediments in Long Island Sound.

Microscopic examination of the fraction  $>125\mu$  showed the most abundant constituent to be quartz. Diatoms, Foraminifera, micas, worm tubes, polychetes, copepods, amphipods, ostracods, gastropods, and pelecypods are common. In the silty sands and clayey silts, the most abundant constituent in the  $125-62\mu$  fraction is elliptical fecal pellets. Diatoms, nematodes, Foraminifera, quartz, and micas are also common. Quantitative counts were made only of the Foraminifera.

#### SIGNIFICANCE OF PARTICLE-SIZE ANALYSES

Since clay-size particles tend to bind organic matter, the clay content of the sediment is often an important factor in governing the distribution and quantity of benthonic organisms. Sanders (1956, p. 404) found the largest infaunal populations in L.I.S. at silt-clay concentrations of 13-25 percent. He was also able to relate the abundance of various infaunal organisms to the particle size of the sediment.

In L.I.S. where the silt and clay content of the sediment is less than 2 percent there are usually no Foraminifera. Otherwise, there is no meaningful relation between the particle size of the sediment and the living Foraminifera. For example, at station 19 the sediment is a pebble sand consisting of 29 percent gravel, 59 percent sand, 8 percent silt, and 4 percent clay; the number of living Foraminifera is 681. At station 14 the sediment is a sand consisting of 13 percent gravel, 82 percent sand, 3 percent silt, and 2 percent clay; the number of living Foraminifera is 441. At station 113 the sediment is a clayey silt consisting of 4 percent gravel, 16 percent sand, 36 percent silt, and 44 percent clay; the number of living Foraminifera is 478. The above stations are all in near-shore areas and although the sediment ranged from pebble sand to clayey silt, all the stations contained a large living population. Some further examples will illustrate the situation in the offshore areas. Station 116 is a silty sand consisting of 0.5 percent gravel, 70 percent sand, 14 percent silt, and 15 percent clay; the number of living Foraminifera is 47. Station 125 is a pebble sand consisting of 54 percent gravel, 40 percent sand, 2 percent silt, and 4 percent clay; the number of living Foraminifera is 48. Station 119 is a clayey silt consisting of 10 percent sand, 44 percent silt, and 45 percent clay; the number of living Foraminifera is 40. These examples and careful examination of the data indicate that particle size has no influence on the numbers of living Foraminifera in L.I.S.

Similarly, the distribution of species cannot be related to particle size of the sediment. For example, at station 12 the sediment is a clayey silt consisting of 11 percent sand, 58 percent silt, and 31 percent clay; the number of living *Elphidium clavatum* is 600, *Buccella frigida* 53, and *eggerella advena* 0. At station 8 the sediment is a clayey silt consisting of 14 percent sand, 55 percent silt, and 30 percent clay; the number of living *E. clavatum* is 0, *B. frigida* 23, and *E. advena* 106. Examination of the data indicates numerous examples of faunal change without any relation to the particle size of the sediment.

The lack of Foraminifera in traverse 5 is puzzling. Stations 54 and 58 contain less than 2 percent silt and clay, but stations 55 and 57 contain over 50 percent while station 56 contains 8 percent. Clearly, the absence of living Foraminifera (stations 54 and 55 contain one individual each) at all these stations cannot be attributed to an insufficient amount of silt and clay.

#### RATIOS OF LIVING TO TOTAL POPULATIONS IN L.I.S.

Phleger (1951) discussed and used the living and total populations of Foraminifera in estimating relative rates of sedimentation in the Gulf of Mexico. Walton (1955) used the ratio of living to dead populations to indicate relative rates of sedimentation in Todos Santos Bay. Phleger (1955) expressed the ratio of living to total populations (L/T) in percent and estimated relative rates of sedimentation in the southeastern Mississippi delta area. The use of an L/T ratio is based on several assumptions which have been discussed in the papers mentioned above. If the living population represents the rate of addition of tests to the sediment and the total population represents this accumulation over a period of time, then the ratio L/T indicates the relative rate of sedimentation providing tests are not removed from the sediment. If sedimentation is rapid, the L/T ratio will be high because empty tests are being rapidly buried.

The frequency distribution for the L/T ratio expressed in percent is shown in figure 21 for all species, *Elphidium clavatum*, *Buccella frigida*, and *eggerella advena*, in the 13 grand stations of traverse 3. The frequency distribution of the L/T ratio of all species has maximum values in the central area of the traverse and minimum values at the ends. It would appear, then, that sedimentation is relatively more rapid in the central areas than near shore.

Let us examine the L/T frequency distribution of all species in greater detail by examining the L/T frequency distributions of the

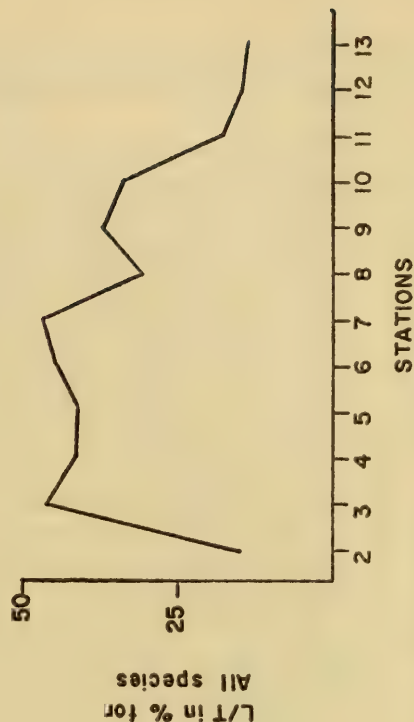
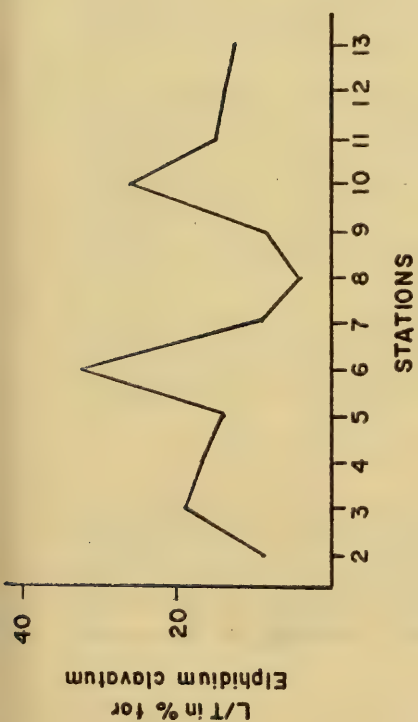
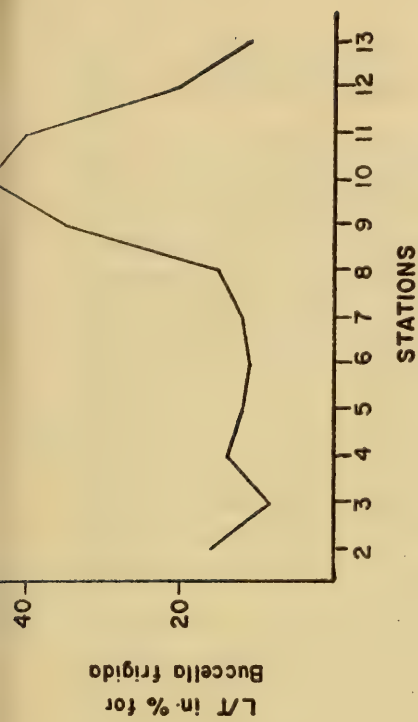


Fig. 21.—Distribution of living population in percent of total population at grand stations.



three abundant species. The L/T frequency distribution of *E. clavatum* has values of less than 20 percent at all stations except 6 and 10. The high at station 6 is due to a slight increase in the living population of *E. clavatum* combined with a slight decrease in the dead population. At station 10 both the living and dead populations are increasing, but the living population is increasing at a greater rate. The L/T ratio of *B. frigida* is less than 20 percent at all stations except 9, 10, and 11. The maximum is the result of an increase in the living population combined with a decrease in the dead population at these stations. The L/T ratio of *E. advena* is greater than 70 percent at all stations except 8, 9, 10, and 11. At stations 8 and 9 the dead population increases whereas the living population remains constant, resulting in lower L/T values. At stations 10 and 11 both the living and dead populations are decreasing, but the living population decreases more rapidly.

The L/T frequency distribution of all species indicates that at stations 3 to 8 the distribution is controlled by the L/T ratio of *E. advena*, the most abundant species in this area. At station 9, the L/T ratio of *B. frigida* becomes important, while at stations 10 and 11 the L/T ratios of *B. frigida* and *E. clavatum* control the distribution. Stations 12 and 13 are in an area where *E. clavatum* is most abundant and its L/T ratio controls the distribution of these stations. Station 2 also has a low L/T value for all species owing to the influence of *E. clavatum*.

If the L/T ratio of all species is an accurate indicator of the relative rate of sedimentation, then the L/T ratios of the component species should show the same pattern. In traverse 3, the L/T ratios of the three abundant species each give a different interpretation of the relative rate of sedimentation. The L/T ratio for *E. advena* is always high, and it is likely that empty tests of this fragile arenaceous species are being destroyed.

Figure 22 shows the L/T ratios expressed in percent for the stations in L.I.S. The values for traverse 3 are seasonal averages. In general, the ratios are higher in the central area (*E. advena* zone).

#### SIGNIFICANCE OF ENVIRONMENTAL FACTORS

I have shown that the number of foraminiferal species increases to the east and that the number of living Foraminifera in the *Eggerella advena* zone of traverse 2 (west) is greater than in traverse 3 (central). It was also observed that the most striking change in the foraminiferal fauna is with depth. Broadly speaking, the fauna can

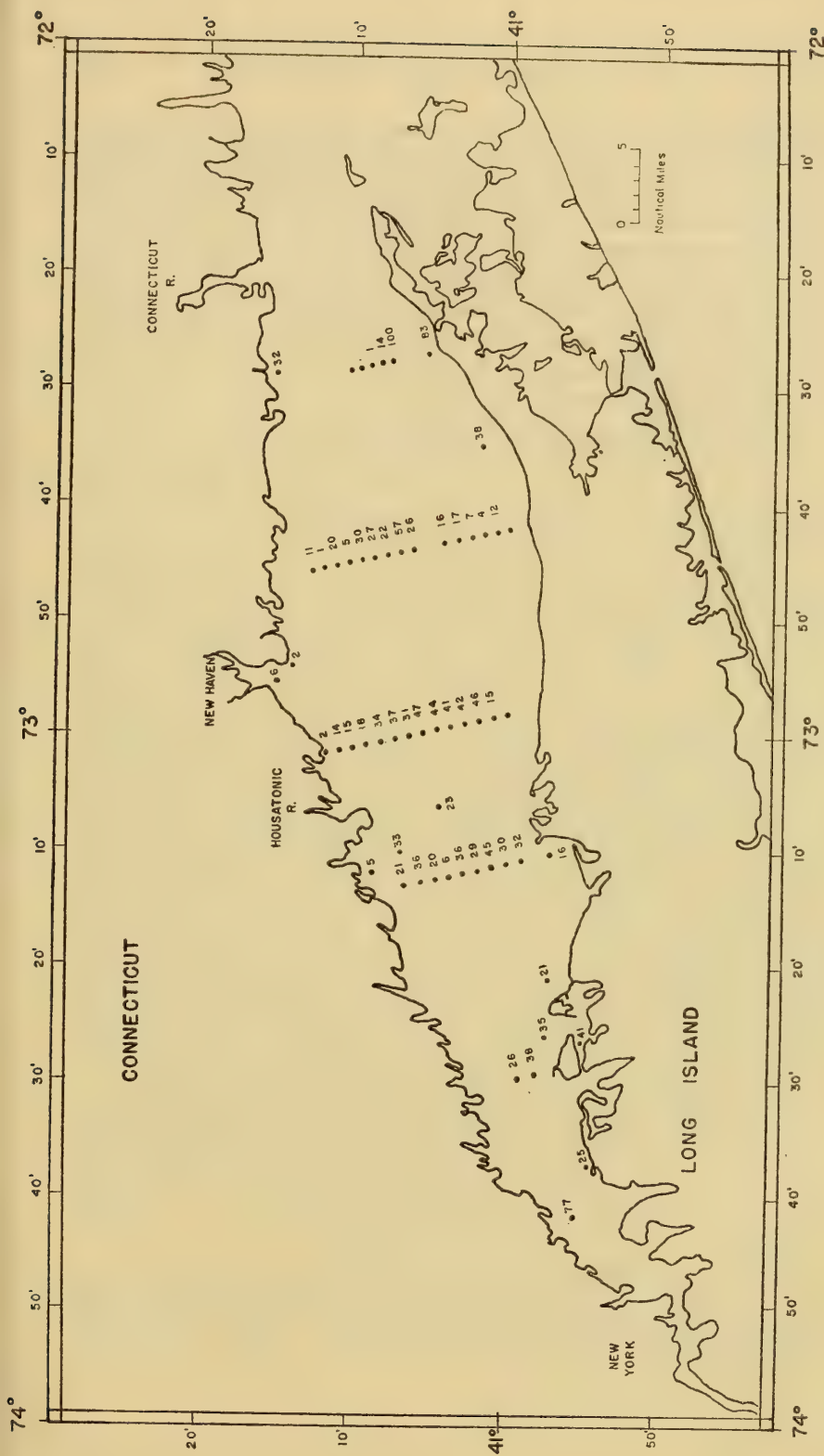


FIG. 22.—Areal distribution of living population in percent of the total population.

be divided into near-shore (<20 m.) and offshore (>20 m.) assemblages. In terms of numbers of living individuals, the near-shore areas (10-20 m.) average 177 per sample, while the offshore areas (20-40 m.) average 62. At depths of less than 10 m. the living population has an average of 335 individuals per sample.

Riley (1959) has shown that the western end of the Sound is usually about 3-5‰ fresher than the eastern end. The increase in foraminiferal species to the east is most likely due to the more oceanic conditions found there and to the proximity of the open ocean from which migration into the Sound can occur.

In L.I.S. the concentration of nutrients and phytoplankton increases to the west (Riley, 1959). The significantly larger living population in the *E. advena* zone of traverse 2 is probably related to the potentially greater food supply in the western area.

To relate the foraminiferal zonation with depth to environmental factors is more difficult. Riley (1956, pp. 17, 18) has shown that the seasonal cycle and range of variation in temperature and salinity at near-shore (8-12 m.) and offshore (19-28 m.) stations in the central part of L.I.S. are about the same. Moreover, the seasonal cycles and range of variation in phosphate, nitrate, and oxygen at near-shore and offshore stations do not show significant differences (Riley and Conover, 1956, pp. 51, 52, 54). Since the Foraminifera are holozoic, the seasonal cycle and amount of nutrients should affect them only insofar as it affects the organisms upon which they feed. Very little is known concerning the oxygen requirements of the Foraminifera. At several stations a strong odor of  $H_2S$  emanated from the black muds in the cores, and at some of these stations the living population was abundant. Riley (1959) has indicated that minimum values of oxygen for bottom water are about 40 percent of saturation. It would appear, then, that although reducing conditions may be prevalent in the sediments below the surface, the sediments at or near the surface (within 1 cm. or so) are not oxygen deficient.

The pH and Eh of the sediments have not been investigated during the present study. McCrone and others (1961) have shown that the pH is usually about neutral, whereas the Eh is negative. They did not indicate any differences between near-shore and offshore stations.

I have already pointed out that in L.I.S. both the distribution of species and the number of living individuals bear no relation to the particle size of the sediment.



Conover (1956, p. 69) reported that the concentration of phytoplankton under a unit area of sea surface is usually greater in the off-shore areas. Although planktonic diatoms were shown to be an important source of food for *Elphidium crispum*, Myers (1943) indicated that this foraminifer fed for the most part on benthonic unicellular plants. No data are available on the distribution or quantity of benthonic microflora in L.I.S. Riley (personal communication) has indicated that calculations from Secchi disc readings indicate that the lower limit of the benthonic microflora in L.I.S. is about 11 m. None of the species in this study is restricted to depths of less than 11 m., but *Elphidium clavatum* is most abundant at depths of less than 10 m. and is relatively rare at depths of greater than 20 m. (fig. 8).

Bradshaw (1955) found that one of the species of foraminifers which he was culturing would feed only on the living diatom *Nitzschia*, whereas another species would accept living and dead flagellates as well. In L.I.S., species of *Nitzschia* are more often found in near-shore areas (Conover, 1956, p. 94). Lee and others (1961) found that an algal flora of eight species of pennate diatoms and three of blue-green algae best supported the species they were culturing. Myers (1943, p. 442) suggested that below the photic zone the growth of bacteria on fecal pellets might constitute an important source of food for the Foraminifera. Apparently the food requirements of the Foraminifera are complex and vary from species to species. Although a given species may accept many kinds of food, it is likely that certain types or associations are more beneficial to it than others. Perhaps in this way niche diversification among benthonic foraminifers is achieved. Because temperature, salinity, nitrate, phosphate, oxygen, pH, Eh, particle size of the sediment, and concentration of phytoplankton do not apparently control the observed depth zonation, I suggest that the foraminiferal species in L.I.S. are selective feeders, and that their depth zonation is, therefore, related to the distribution of the material upon which they feed. The environmental parameters which might control the distribution of such material are not readily apparent from this study.

#### PALEOECOLOGIC IMPLICATIONS

Most of the sediments in L.I.S. are clayey silts and silty sands. They are black in color, are high in organic content, and show no stratification. Ellis (1962) has indicated that these muds would



become "... black silty or sandy shales containing abundant pyrite or marcasite."

If the sediments of L.I.S. and the fauna contained therein were preserved, the Foraminifera could be used to reconstruct the general aspects of the environment. I have shown that the distribution of the living and total populations closely approximate one another. Therefore, a study of the total population would in general give an accurate account of foraminiferal distribution in L.I.S. The low number of species per sample and the dominance by a single species would indicate a restricted marine environment. The lack of planktonic forms would substantiate this. If the species living in L.I.S. today were still living when the hypothetical fossil fauna was studied, a knowledge of the distribution of such forms as *Reophax dentaliniformis* and *R. nana* would also indicate a restricted or bay environment. The increase in numbers of species to the east would indicate the approach of more oceanic conditions in that direction. The distribution of the abundant species would allow the future paleontologist to distinguish between offshore and near-shore environments and he could, thereby, reconstruct the former geographic configuration of the Sound. Even if the relatively fragile tests of *Eggerella advena* were destroyed, offshore and near-shore environments could still be distinguished by the relative abundances of *Elphidium clavatum* and *Buccella frigida*.

In short, providing the sediments could be correlated and the future paleontologist knew as much about the Foraminifera as we do now, the general environmental features of the fossilized sediments of L.I.S. could be worked out.

#### SYSTEMATIC CATALOG OF SPECIES

Most of the foraminiferal species found in L.I.S. have been adequately described by Cushman (1944) and Parker (1952a, 1952b). No detailed descriptions or synonymies are given because the taxonomy of the species involved is fairly straightforward. The *Elphidium* group is an exception and some notes on the author's views are offered. A brief account of the distribution of each species is included.

##### Family REOPHACIDAE

##### Genus REOPHAX Montfort, 1808

##### REOPHAX DENTALINIFORMIS Brady

##### Plate 1, figure 1

*Reophax dentaliniformis* Brady, Quart. Journ. Micr. Sci., vol. 21, p. 49, 1881.—

PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 457, pl. 1, fig. 19, 1952.

Living and dead individuals belonging to this species occur with low frequencies throughout L.I.S. This species is not, however, found at depths of less than 13 m. Parker (1952b) suggested that *R. dentaliniformis* may be confined to sediments containing mud. The present study substantiates her suggestion somewhat. *R. dentaliniformis* is often found in the offshore stations which are usually muds. It was not found, however, at stations 125 and 80, which are offshore sands. As mentioned above, this species is conspicuously absent from all shallow stations including those whose particle-size distribution is similar to the offshore muds.

#### REOPHAX NANA Rhumbler

Plate 1, figure 2

*Reophax nana* RHUMBLER, Ergeb. Plankton-Exped. Humboldt Stiftung, Bd. 3, pt. 2, p. 471, pl. 8, figs. 6-12, 1913.—PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 457, pl. 1, figs. 14, 15, 1952.

Living and dead individuals of this species are found in L.I.S., but their occurrence is scattered and never comprises more than 2 percent of the total fauna.

#### Family LITUOLIDAE

Genus **AMMOSCALARIA** Hoglund, 1947

**AMMOSCALARIA** cf. **FLUVIALIS** Parker

Plate 1, figure 3

A few specimens that probably belong to this species, which was described by Parker (1952b, p. 444, pl. 1, figs. 24, 25), were found at station 98a in Lloyd's Harbor at a depth of 4 m. None of the specimens was living at the time of collection, and no complete individuals were observed. Most of the specimens were so fragile that they disintegrated when the sample was dried.

#### Family VALVULINIDAE

Genus **EGGERELLA** Cushman, 1933

**EGGERELLA** **ADVENA** (Cushman)

Plate 1, figures 4, 5

*Verneuilina advena* CUSHMAN, Contr. Can. Biol., No. 9, p. 141, 1921.

*Eggerella advena* (Cushman) PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 447, pl. 2, fig. 3, 1952.

This species is found throughout L.I.S., but has its greatest abundance in the central areas of the traverses. In the central areas the

relative abundance of *E. advena* in the living population is usually 25-30 percent greater than it is in the total population. The L/T ratio of this species is usually much higher than it is for the other common species, and it is likely that specimens of this species may be fragile enough to be destroyed after death. Specimens of *E. advena* are almost entirely confined to the 0.125-0.062 mm. size fraction.

Family MILIOLIIDAE

Genus QUINQUELOCULINA d'Orbigny, 1826

QUINQUELOCULINA SEMINULUM (Linné)

Plate 1, figure 6

*Serpula seminulum* LINNÉ, Syst. Nat., ed. 10, p. 786, 1758.

*Quinqueloculina seminula* (Linné) PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 456, pl. 2, figs. 7a, b, 1952.

The individuals from L.I.S. are smaller than the figured specimen of Parker (1952b). All specimens have a simple tooth, lack a neck, and are similar in overall shape.

Living and dead individuals of this species are found with very low frequencies in all parts of L.I.S.

QUINQUELOCULINA SEMINULUM (Linné) var. JUGOSA Cushman

Plate 1, figure 7

*Quinqueloculina seminula* (Linné) var. *jugosa* Cushman, CUSHMAN Lab. Foram. Res. Spec. Publ. 12, pp. 13-14, pl. 2, fig. 15, 1944.—PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 456, pl. 2, figs. 8a, b, 1952.

One live specimen belonging to this variety was found at station 1, and four dead specimens were found at station 20.

Family OPTHALMIDIIDAE

Genus CORNUSPIRA Schultze, 1854

CORNUSPIRA PLANORBIS Schultze

Plate 1, figure 8

*Cornuspira planorbis* SCHULTZE, Organismus Polythal., p. 40, pl. 2, fig. 21, 1854.—CUSHMAN and TODD, Cushman Lab. Foram. Res., Spec. Publ. 21, p. 7, pl. 1, fig. 24, 1947.—TODD and LOW, Contr. Cushman Found. Foram. Res., vol. 12, p. 15, pl. 1, fig. 9, 1961.

A few dead specimens were found at stations 47, 48, 59, 114, and 133. Five living individuals were found at station 125.

## Family TROCHAMMINIDAE

## Genus TROCHAMMINA Parker and Jones, 1959

## TROCHAMMINA COMPACTA Parker

*Trochammina compacta* PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 458-459, pl. 2, figs. 13a, b, 14a, b, 15a, b, 1952.

A few living representatives of this species were found at stations 48, 62, and 71. One dead specimen was found at station 51. The specimens were most fragile and when dried became distorted.

## TROCHAMMINA INFLATA (Montagu)

Plate 1, figures 9a, 9b

*Nautilus inflatus* MONTAGU, Testacea Britannica, Suppl., p. 81, pl. 18, fig. 3, 1808.  
*Trochammina inflata* (Montagu) PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 459, pl. 3, figs. 1a, b, 1952.

One dead specimen referable to this species was found at station 59.

## TROCHAMMINA LOBATA Cushman

Plate 1, figure 10, plate 2, figure 1

*Trochammina lobata* CUSHMAN, 1944, Cushman Lab. Foram. Res., Spec. Publ. 12, p. 18, pl. 2, fig. 10, 1944.—PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, pp. 459-460, pl. 3, figs. 2a, b, 1952.

One dead specimen belonging to this species was found at station 48.

## TROCHAMMINA SQUAMATA Parker and Jones

Plate 2, figures 2a, 2b

*Trochammina squamata* PARKER and JONES, Philos. Trans. Roy. Soc. London, vol. 155, p. 407, pl. 15, figs. 30, 31a, b, c, 1865.  
*Trochammina propria* CUSHMAN, Cushman Lab. Foram. Res. Spec. Publ. 12, p. 19, pl. 2, fig. 11, 1944.  
*Trochammina squamata* Parker and Jones, and related species, PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 460, pl. 3, figs. 4a, b, 1952.

This species is somewhat variable in form. The test is often fragile, and some specimens have very indistinct morphological features. Most individuals are concavo-convex, the dorsal side being convex. The umbilicus is usually deep, and the sutures on the ventral side become curved as they approach the periphery. The final chamber on the ventral side is often inflated.

Living and dead individuals of *T. squamata* are widely distributed in



L.I.S. but were not found in the westernmost traverses. This species always occurs with low frequencies.

Family LAGENIDAE

Genus **FISSURINA** Reuss, 1850

**FISSURINA LAEVIGATA** Reuss

Plate 2, figure 3

*Fissurina laevigata* REUSS, Denkschr. Akad. Wiss. Wien, vol. 1, p. 366, pl. 46, fig. 1, 1849.

*Entosolena laevigata* (Reuss), CUSHMAN, Cushman Lab. Foram. Res. Spec. Publ. 12, p. 28, pl. 4, fig. 12, 1944.

Living and dead individuals belonging to this species were found throughout L.I.S. *F. laevigata* usually accounts for no more than a few specimens in any sample.

Family POLYMORPHINIDAE

Genus **PSEUDOPOLYMORPHINA** Cushman and Ozawa, 1938

**PSEUDOPOLYMORPHINA NOVANGLIAE** (Cushman)

Plate 2, figure 4

*Polymorphina lactea* (Walker and Jacob) var. *novangliae* CUSHMAN, U. S. Nat. Mus. Bull. 104, pt. 4, p. 146, pl. 39, figs. 6-8, 1923.

*Pseudopolymorphina novangliae* (Cushman) PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 455, pl. 3, figs. 11, 12, 1952.

Living and dead individuals belonging to this species are found with very low frequencies in all parts of L.I.S.

Family NONIONIDAE

Genus **NONIONELLA** Cushman, 1926

**NONIONELLA ATLANTICA** Cushman

Plate 2, figures 5a, 5b

*Nonionella atlantica* CUSHMAN, Contr. Cushman Lab. Foram. Res., vol. 23, pt. 4, p. 90, pl. 20, figs. 4, 5, 1947.—PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 453, pl. 3, figs. 15a, b, 1952.

Two dead specimens belonging to this species were found in L.I.S. One came from station 48, the other from 106.

Family ELPHIDIIDAE

Genus **ELPHIDIUM** Monfort, 1808

**ELPHIDIUM CLAVATUM** Cushman

Plate 2, figures 6, 7; plate 3, figures 1, 2

*Elphidium incertum* (Williamson) var. *clavatum* CUSHMAN, U. S. Nat. Mus. Bull. 104, pt. 7, p. 20, pl. 7, figs. 10a, b, 1930.

*Elphidium incertum* (Williamson) and variants, PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 448, pl. 3, figs. 14, 16, 17; pl. 4, figs. 1, 2, 1952.

*Elphidium clavatum* Cushman, emend. LOEBLICH and TAPPAN, Smithsonian Misc. Coll., vol. 121, No. 7, pp. 98-99, pl. 19, figs. 8-10, 1953.

The forms included under this species exhibit a very wide range of variation. Adult specimens have 8 to 11 chambers in the final whorl. Individuals vary in color and transparency from brown translucent to white opaque. All specimens have short retral processes, but their number and arrangement vary. The typical *E. clavatum* form (brown translucent) has several umbilical bosses which sometimes extend part way up the sutures or may form a single umbonal mass. White opaque individuals often have several distinct umbilical bosses which are sometimes fused by the addition of shell material so that only irregular slits appear in the umbilical region. Examination of many specimens indicates that the range of variation is in all respects continuous. Moreover, when the  $\text{CaCO}_3$  of the test is dissolved, all the specimens examined showed a thick brown organic inner lining which is not found in any of the other species in this area.

Cushman (1930) originally described this species as a variety of *E. incertum* (Williamson). Loeblich and Tappan (1953) raised the variety to specific rank and discussed its relation to *E. incertum*. They found on slides in the U. S. National Museum referred to *E. incertum* a mixture of several species of *Elphidium*, none of which matched Williamson's original figure. The hypotypes of *E. clavatum* deposited at the U. S. National Museum by Loeblich and Tappan (1953) are identical with the brown translucent form of *E. clavatum* described above. White opaque individuals with retral processes and irregular sutures and/or umbonal bosses have been in the past and are still referred by various workers to *E. incertum*. Parker (1952b) recognized that the variation in morphology between the typical *E. clavatum* and what has been referred to as *E. incertum* is continuous. She chose, however, to call the species *E. incertum* (Williamson) and variants. My views are similar to hers, but I believe it is best to refer to this species as *E. clavatum* because none of the morphological types so frequently referred to *E. incertum* matches Williamson's original figure.

This species is most abundant in L.I.S. It occurs in all areas, but is far more abundant at depths of less than 15 m. In shallow waters this species comprises about 90 percent of the total population, whereas in the central part of L.I.S. it makes up about 20-35 percent of the total population. In the shallow areas the living population is usually 5-10 percent smaller than the total population, but in the central area it is often 20 percent smaller.

**ELPHIDIUM PAUCILOCULUM (Cushman)**

## Plate 3, figure 3

*Nonion pauciloculum* CUSHMAN, Cushman Lab. Foram. Res., Spec. Publ. 12, p. 24, pl. 3, fig. 25, 1944.

*Elphidium subarcticum* CUSHMAN, Cushman Lab. Foram. Res., Spec. Publ. 12, p. 27, pl. 3, figs. 34, 35, 1944.—PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 9, p. 412, pl. 5, fig. 9, 1952a.—PARKER, *ibid.*, vol. 106, No. 10, p. 449, pl. 4, figs. 3-6, 8, 1952b.

In the material from L.I.S. some specimens have wide white bands of amorphous material covering the sutural areas. Others have a deep slit along the suture and white bands on either side. Still others exhibit a combination of the two. Retral processes were observed on some of the specimens. The holotype of the species described by Cushman as *N. pauciloculum* is a form with depressed slitlike sutures, while the holotype on *E. subarcticum* is a form with retral processes. In L.I.S. the range of variation between these extremes is continuous. Parker (1952a) observed the same relationships in her study of the fauna from the Gulf of Maine. However, she chose to use the name *E. subarcticum*. Cushman (1944) described both species in the same paper, but *N. pauciloculum* was described on an earlier page and therefore has priority.

This species is common throughout L.I.S. It usually comprises less than 10 percent of the total population, although at a few stations it comprises as much as 30 percent of the living population.

**ELPHIDIUM TISBURYENSE (Butcher)**

## Plate 3, figure 4

*Nonion tisburyensis* BUTCHER, Contr. Cushman Lab. Foram. Res., vol. 24, p. 22, text figs. 1-3, 1948.

This species closely resembles *E. orbiculare* (Brady). It differs from the latter in that the individual chambers are more inflated and the test is not as thick and orbicular. Nevertheless, the two species are morphologically very similar, and further study on the expected range of variation is desirable. The material from L.I.S. was identified as *E. tisburyense* because as a group the specimens more closely resemble this form.

A few living and dead individuals of this species were found at stations 59 and 98a. A few dead individuals were found at stations 19, 74, and 123.

**ELPHIDIUM VARIUM Buzas**

## Plate 3, figure 5

*Elphidium incertum* (Williamson) CUSHMAN, (non *Polystomella umbilicatula* var. *incerta* Williamson, 1858), Cushman Lab. Foram. Res., Spec. Publ. 23, pp. 56-57, pl. 6, fig. 7a, b, 1948.

*Elphidium varium* BUZAS, Smithsonian Misc. Coll. vol. 145, No. 8, p. 21, pl. 2, fig. 7; pl. 3, figs. 1, 2a, 2b, 1965.

This species is translucent to opaque in appearance. It is finely perforate, and only some individuals have retral processes. The translucent individuals can be easily confused with *E. pauciloculum* or *E. tisburyense*, whereas the opaque individuals with retral processes can be confused with opaque specimens of *E. clavatum*. This species does, however, form a distinct recognizable morphologic group. Moreover, the wall structure of *E. varium* is granular, whereas the other species of *Elphidium* in L.I.S. are all radial.

This species is common in all areas of L.I.S. but usually comprises less than 10 percent of the total population. Living individuals were found in all areas with low frequencies. Some of the living individuals were found in cysts composed of quartz and organic matter.

## Family BULIMINIDAE

Genus **BOLIVINA** d'Orbigny, 1839**BOLIVINA VARIABILIS** (Williamson)

## Plate 3, figure 6

*Textularia variabilis* WILLIAMSON, Rec. Foram. Great Britain, p. 76, pl. 6, figs. 162, 163, 1858.

*Bolivina variabilis* (Williamson) PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 445, pl. 4, fig. 12, 1952.

A few living specimens belonging to this species were found at stations 76, 78, 63, 64, 86, and 125'. A few dead individuals were found at stations 64 and 132.

Genus **VIRGULINA** d'Orbigny, 1826**VIRGULINA FUSIFORMIS** (Williamson)

## Plate 3, figure 7

*Bulimina pupoides* d'Orbigny var. *fusiformis* WILLIAMSON, Rec. Foram. Great Britain, p. 63, pl. 5, figs. 129, 130, 1858.

*Virgulina fusiformis* (Williamson) PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 461, pl. 4, fig. 10, 1952.

Living and dead individuals of this species were found with low frequencies in traverses 3 and 4 and at station 59.



## Family ROTALIIDAE

## Genus AMMONIA Brunnich, 1771

## AMMONIA BECCARII (Linne)

Plate 4, figures 1a, 1b

*Nautilus beccarii* LINNÉ, Syst. Nat., ed. 10, p. 710, 1758.*Rotalia beccarii* (Linné) PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, pp. 457-458, pl. 5, figs. 5a, b, 7a, b, 8a, b, 1952.

Living and dead individuals of this species are found with low frequencies in traverses 2 and 4 as well as at stations 98 and 17.

## Genus BUCCELLA Andersen, 1952

## BUCCELLA FRIGIDA (Cushman)

Plate 4, figures 2a, 2b, 3a, 3b

*Pulvinulina frigida* CUSHMAN, Contr. Can. Biol., No. 9 (1921), p. 12 (144), 1922.*Eponides frigidus* (Cushman) PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, pp. 449, pl. 5, figs. 2a, b, 1952.*Eponides frigidus* (Cushman) var. *calidus* Cushman and Cole, PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, p. 450, pl. 5, figs. 3a, b, 1952.*Buccella frigida* (Cushman) ANDERSEN, Journ. Washington Acad. Sci., vol. 42, No. 5, p. 144, figs. 4a-c, 5, 6a-c, 1952.

This species is very common in L.I.S. Living and dead specimens are found at almost all stations. The living population has its maximum frequency on the north side of traverses 2 and 3 about 3-5 miles offshore at a depth of 15-25 m. In traverse 4, *B. frigida* is more abundant, and the living population is developed on both the north and south sides of the Sound. The frequency distribution of the total population has fewer maxima and usually makes up 20-30 percent of the total population in the offshore stations.

## Genus POROEPONIDES Cushman, 1944

## POROEPONIDES LATERALIS (Terquem)

Plate 4, figures 4a, 4b

*Rosalina lateralis* TERQUEM, Mem. Soc. Geol. France, ser. 3, vol. 1, Mem. 3, p. 25, pl. 2, figs. 11a-c, 1878.*Poroeponides lateralis* (Terquem) PARKER, Bull. Mus. Comp. Zool., vol. 106, No. 10, pp. 453-454, pl. 5, figs. 6a, b, 1952b.

One living specimen was found at station 54. One dead specimen was found at station 42 and another at station 45.

### GENERAL SUMMARY

This study is based on 220 samples obtained during 14 cruises on Long Island Sound. Living and total populations were counted in 161 samples, while particle-size analyses were made on 59.

Statistical analyses of 12 paired samples indicate that the species investigated are more homogeneous in the living than in the total population, and the number of living individuals per sample can be more reliably estimated than the total number of individuals. The offshore area is more homogeneous and gives a better estimate of the number of individuals per sample than the near-shore area.

Of the 23 species found in the Sound, 19 were represented by living individuals. The number of species increases as the more oceanic waters of Block Island Sound are approached. *Elphidium clavatum*, *Buccella frigida*, and *Eggerella advena* comprise about 75 percent of the living as well as of the total population. Three zones are defined by the change in relative abundance of these species with depth. In the living population, the mean depth of stations in the *E. clavatum*, *B. frigida*, and *E. advena* zones is 12 m., 25 m., and 29 m. respectively. The distribution of the total population closely approximates that of the living population.

In the *E. advena* zone, a significantly greater number of living individuals occurs in the western area than in the central area. This difference probably is related to the greater concentration of nutrients and phytoplankton in the western part of the Sound.

In seasonal sampling of the central area, a significant maximum for the living population in the *E. advena* zone occurred in June 1962. *E. advena* was most abundant in October 1961 but did not show any maximum in early autumn 1962. Maximum seasonal abundances correlate in a general way with the seasonal cycle of the phytoplankton and with times of maximum temperature. Juveniles of *E. clavatum* were found throughout the year, and probably only the rate of reproduction varies.

Most of the sediments are silty sands and clayey silts. The distribution of species, as well as numbers of living individuals, bear no relation to the particle size of the sediment. Living to total population ratios of the abundant species indicate that this ratio is not a reliable indicator of relative rates of sedimentation in the Sound.

The distribution of the Foraminifera with depth cannot be related to temperature, salinity, phosphate, nitrate, oxygen, pH, Eh, concentration of phytoplankton, or particle size of the sediment. It is suggested that the foraminifers in the Sound are selective feeders, and their distribution is related to the distribution of the material upon which they feed.

TABLE 1.—Chi-square analyses of sample pairs. The actual number of individuals observed is columned under (o). The expected frequency (e) of a species in a sample is calculated by multiplying the sum of the species row by the sum of the sample column and dividing by the total sum of both samples. Chi-square is calculated by the formula  $\sum_{\text{cells}} \frac{(o - e)^2}{e}$ .

#### SAMPLE PAIR 10-10'

Total Population							
	10 o	10' o	Total	10 e	10' e	$\frac{(o - e)^2}{e}$	$\frac{(o - e)^2}{e}$
1 .....	671	873	1,544	739.12	804.81	6.28	5.78
2 .....	266	163	429	205.38	223.62	17.89	16.43
3 .....	43	31	74	35.43	38.57	1.62	1.48
Totals ....	980	1,067	2,047	979.93	1,067.00	25.79	23.69

$$\chi^2_2 = 49.48 *$$

#### Live Population

	10 o	10' o	Total	10 e	10' e	$\frac{(o - e)^2}{e}$	$\frac{(o - e)^2}{e}$
1 .....	288	484	772	364.71	407.29	16.13	14.45
2 .....	203	71	274	129.44	144.56	41.80	37.43
3 .....	23	19	42	19.84	22.16	0.50	0.45
Totals ....	514	574	1,088	513.99	574.01	58.43	52.33

$$\chi^2_2 = 110.76 *$$

#### SAMPLE PAIR 14-14'

Total Population							
	14 o	14' o	Total	14 e	14' e	$\frac{(o - e)^2}{e}$	$\frac{(o - e)^2}{e}$
1 .....	1,678	2,664	4,322	1,639.21	2,702.22	0.92	0.54
2 .....	9	117	126	47.79	78.78	31.82	18.54
Totals ....	1,687	2,781	4,448	1,687.00	2,781.00	32.74	19.08

$$\chi^2_1 = 51.82 *$$

\* Significant at the 95 percent level.

#### Live Population

	14 o	14' o	Total	14 e	14' e	$\frac{(o - e)^2}{e}$	$\frac{(o - e)^2}{e}$
1 .....	404	191	595	389.18	205.82	0.56	1.07
2 .....	29	38	67	43.82	23.18	5.01	9.48
Totals ....	433	229	662	433.00	229.00	5.57	10.55

$$\chi^2_1 = 16.12 *$$



TABLE 1—*Continued*  
SAMPLE PAIR 24-24'

Total Population							
	24 <i>o</i>	24' <i>o</i>	Total	24 <i>e</i>	24' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	91	11	102	83.90	18.10	0.60	2.78
2 .....	103	0	103	84.72	18.28	3.94	18.28
3 .....	47	41	88	72.38	15.62	8.90	41.24
Totals ....	241	52	293	241.00	52.00	13.44	62.30

$$\chi^2_2 = 75.74 *$$

Live Population							
	24 <i>o</i>	24' <i>o</i>	Total	24 <i>e</i>	24' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	10	3	13	9.39	3.60	0.04	0.10
2 .....	42	0	42	30.35	11.65	4.47	11.65
3 .....	34	30	64	46.25	17.75	3.24	8.45
Totals ....	86	33	119	85.99	33.00	7.75	20.20

$$\chi^2_2 = 27.95 *$$

\* Significant at the 95 percent level.

SAMPLE PAIR 59-59'

Total Population							
	59 <i>o</i>	59' <i>o</i>	Total	59 <i>e</i>	59' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	197	195	392	190.93	201.07	0.19	0.18
2 .....	9	10	19	9.25	9.74	0.01	0.01
3 .....	20	33	53	25.81	27.18	1.31	1.25
Totals ....	226	238	464	225.99	237.99	1.51	1.44

$$\chi^2_2 = 2.95$$

Live Population							
	59 <i>o</i>	59' <i>o</i>	Total	59 <i>e</i>	59' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	63	61	124	58.66	65.34	0.32	0.29
3 .....	16	27	43	20.34	22.66	0.93	0.83
Totals ....	79	88	167	79.00	88.00	1.25	1.12

$$\chi^2_1 = 2.37$$

TABLE 1—*Continued*  
SAMPLE PAIR 102-102'

Total Population							
	102 <i>o</i>	102' <i>o</i>	Total	102 <i>e</i>	102' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	187	151	338	172.73	165.26	1.18	1.23
2 .....	44	65	109	55.70	53.29	2.46	2.57
3 .....	0	5	5	2.56	2.44	2.56	2.68
Totals ....	231	221	452	230.99	220.99	6.20	6.48

$$\chi^2_2 = 12.68 *$$

\* Significant at the 95 percent level.

Live Population					
	102 <i>o</i>	102' <i>o</i>	Total	102 <i>e</i>	102' <i>e</i>
1 .....	3	3	6	1.56	4.43
2 .....	3	9	12	3.13	8.87
3 .....	0	5	5	1.30	3.70
Totals ....	6	17	23	5.99	17.00

SAMPLE PAIR 104-104'

Total Population							
	104 <i>o</i>	104' <i>o</i>	Total	104 <i>e</i>	104' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	80	38	118	75.63	42.37	0.25	0.45
2 .....	60	37	97	62.17	34.83	0.08	0.20
3 .....	1	4	5	3.20	1.80	1.51	3.20
Totals ....	141	79	220	141.00	79.00	1.84	3.85

$$\chi^2_2 = 5.69$$

Live Population							
	104 <i>o</i>	104' <i>o</i>	Total	104 <i>e</i>	104' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	2	3	5	2.08	2.92	0.00	0.00
2 .....	2	0	2	0.83	1.17		
3 .....	1	4	5	2.08	2.92	0.56	0.40
Totals ....	5	7	12	4.99	7.01	0.56	0.40

$$\chi^2_1 = 0.96$$

TABLE 1—*Continued*

## SAMPLE PAIR 106-106'

Total Population							
	106 <i>o</i>	106' <i>o</i>	Total	106 <i>e</i>	106' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	16	13	29	17.61	11.39	0.15	0.23
2 .....	7	5	12	7.28	4.71	0.01	0.02
3 .....	11	4	15	9.11	5.89	0.39	0.61
Totals ....	34	22	56	34.00	21.99	0.55	0.86

$$\chi^2_2 = 1.41$$

Live Population					
	106 <i>o</i>	106' <i>o</i>	Total	106 <i>e</i>	106' <i>e</i>
1 .....	2	1	3	2.12	0.88
2 .....	2	1	3	2.12	0.88
3 .....	8	3	11	7.76	3.24
Totals ....	12	5	17	12.00	5.00

## SAMPLE PAIR 108-108'

Total Population							
	108 <i>o</i>	108' <i>o</i>	Total	108 <i>e</i>	108' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	49	37	86	40.00	46.00	2.02	1.76
2 .....	19	31	50	23.26	26.74	0.78	0.68
3 .....	12	24	36	16.74	19.26	1.34	1.17
Totals ....	80	92	172	80.00	92.00	4.14	3.61

$$\chi^2_2 = 7.75 *$$

\* Significant at the 95 percent level.

Live Population					
	108 <i>o</i>	108' <i>o</i>	Total	108 <i>e</i>	108' <i>e</i>
1 .....	2	0	2	0.88	1.13
2 .....	2	2	4	1.75	2.25
3 .....	10	16	26	11.38	14.62
Totals ....	14	18	32	14.01	18.00

TABLE 1—*Continued*  
SAMPLE PAIR 125-125'

Total Population							
	125 <i>o</i>	125' <i>o</i>	Total	125 <i>e</i>	125' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	124	128	252	127.12	124.88	0.08	0.08
2 .....	21	8	29	14.63	14.37	2.77	2.82
3 .....	25	31	56	28.25	27.75	0.37	0.38
Totals ....	170	167	337	170.00	167.00	3.22	3.28

$$\chi^2_2 = 6.50 *$$

Live Population							
	125 <i>o</i>	125' <i>o</i>	Total	125 <i>e</i>	125' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	12	14	26	10.33	15.67	0.27	0.18
2 .....	1	2	3	1.19	1.81		
3 .....	16	28	44	17.48	26.52	0.12	0.08
Totals ....	29	44	73	29.00	44.00	0.39	0.26

$$\chi^2_1 = 0.65$$

\* Significant at the 95 percent level.

SAMPLE PAIR 129-129'

Total Population							
	129 <i>o</i>	129' <i>o</i>	Total	129 <i>e</i>	129' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	11	37	48	16.55	31.45	1.25	0.98
2 .....	4	17	21	7.24	13.76	1.45	0.76
3 .....	25	22	47	16.21	30.79	4.76	8.79
Totals ....	40	76	116	40.00	76.00	7.46	10.53

$$\chi^2_2 = 17.99 *$$

Live Population							
	129 <i>o</i>	129' <i>o</i>	Total	129 <i>e</i>	129' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	2	3	5	2.07	2.93	0.00	0.00
2 .....	0	4	4	1.67	2.34		
3 .....	15	17	32	13.27	18.73	0.22	0.16
Totals ....	17	24	41	17.01	24.00	0.22	0.16

$$\chi^2_1 = 0.38$$



TABLE 1—*Continued*  
SAMPLE PAIR 131-131'

	131 <i>o</i>	131' <i>o</i>	Total	131 <i>e</i>	131' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	55	69	124	61.73	62.27	0.73	0.73
2 .....	42	27	69	34.35	34.65	1.70	1.69
3 .....	16	18	34	16.92	17.07	0.05	0.05
Totals ....	113	114	227	113.00	113.99	2.48	2.47

$$\chi^2_2 = 4.95$$

\* Significant at the 95 percent level.

Live Population

	131 <i>o</i>	131' <i>o</i>	Total	131 <i>e</i>	131' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	11	13	24	12.00	12.00	0.08	0.08
2 .....	5	1	6	3.00	3.00	1.33	1.33
3 .....	7	9	16	8.00	8.00	0.12	0.12
Totals ....	23	23	46	23.00	23.00	1.53	1.53

$$\chi^2_2 = 3.06$$

SAMPLE PAIR 133-133'

Total Population

	133 <i>o</i>	133' <i>o</i>	Total	133 <i>e</i>	133' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	202	161	363	201.74	161.26	0.00	0.00
2 .....	101	78	179	99.48	79.52	0.02	0.03
3 .....	1	4	5	2.78	2.22	1.14	1.43
Totals ....	304	243	547	304.00	243.00	1.16	1.46

$$\chi^2_2 = 2.62$$

Live Population

	133 <i>o</i>	133' <i>o</i>	Total	133 <i>e</i>	133' <i>e</i>	$\frac{(o-e)^2}{e}$	$\frac{(o-e)^2}{e}$
1 .....	3	4	7	2.67	4.33	0.04	0.02
2 .....	4	8	12	4.57	7.43	0.07	0.04
3 .....	1	1	2	0.76	1.24		
Totals ....	8	13	21	8.00	13.00	0.11	0.06

$$\chi^2_1 = 0.17$$

TABLE 2.—*Binomial test on numbers of individuals in sample pairs.*

Sample pair	Live No.	$\bar{x}$	Total No.	$\bar{x}$	Vol. Live No. ml. corrected	$\bar{x}$	Total No. corrected	$\bar{x}$
10 .....	527		1002		11.0	479	911	
10' .....	591	-1.88*	1127	2.69	11.5	513	890	-1.56*
14 .....	441		1786		12.1	364	1476	
14' .....	234	8.01	2796	14.91	13.4	175	2086	-10.21
24 .....	95		258		18.3	52	141	
24' .....	36	5.24	60	11.15	14.6	25	41	7.49
59 .....	86		269		13.5	64	199	
59' .....	97	-0.74*	282	-0.51*	13.7	71	206	-0.30*
102 .....	7		276		15.5	5	178	
102' .....	19	-2.16	245	1.40*	14.2	14	173	0.32*
104 .....	6		165		17.2	3	96	
104' .....	10	-0.75*	115	3.05	15.8	6	73	1.85*
106 .....	16		51		14.8	11	34	
106' .....	7	2.08	29	2.57	17.7	4	16	2.68
108 .....	18		99		19.7	9	50	
108' .....	20	-0.16*	104	-0.28*	19.0	10	55	-0.39*
125 .....	48		205		11.2	43	183	
125' .....	64	-1.42*	211	-0.24*	13.0	49	162	1.18*
129 .....	26		57		14.8	18	38	
129' .....	45	-2.14	112	-4.15	18.9	24	59	-2.03
131 .....	28		127		18.3	15	69	
131' .....	31	-0.26*	131	-0.19*	15.4	20	85	-1.21*
133 .....	8		345		13.6	6	254	
133' .....	15	1.25*	264	3.32	13.7	11	193	2.93

\* Significant at the 95 percent level.

TABLE 3.—Distribution of the Foraminifera in percent of the living and total populations. Frequencies of less than 1 percent are tabulated to the nearest tenth of a percent. X denotes a frequency of less than one-tenth of a percent.

TRAVERSE STATIONS	2																			
	110	111	114	116	117	118	119	120	121	122	123	124	125	125'	112	113	114	114'	15	15'
<i>Ammonia beccarii</i>	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T
<i>Ammonia cf. fluviatilis</i>																				
<i>Bolivina variabilis</i>																				
<i>Buccella frigida</i>	31	35	4	9	8	2	6	21	1	10	5	29	6	25	54	21	7	7	10	11
<i>Cornuspira planorbis</i>																				
<i>Eggerella advena</i>	34	20	22	11	10	3	68	26	59	27	92	63	60	27	19	8	8	1	3	9
<i>Elphidium clavatum</i>	11	29	44	55	54	70	8	52	6	27	2	14	12	30	73	62	31	67	80	83
<i>E. pauciloculum</i>	6	5	11	11	18	10	4	2	12	9	2	2	4	2	8	4	7	4	5	5
<i>E. tisburyensis</i>																				
<i>E. varium</i>	6	4	11	5				6	6	7	1	3	5	3	1	3	6	2	5	4
<i>Fissurina laevigata</i>																				
<i>Nonionella atlantica</i>	.8																			
<i>Parasponides lateralis</i>																				
<i>Pseudopolymorphina novaezooe</i>																				
<i>Quinqueloculina seminula</i>																				
<i>Q. seminula var. jugosa</i>																				
<i>Reophax dentatiformis</i>	3	2	4	1				4	2	12	7	1	1	8	3					
<i>R. nona</i>																				
<i>Trochammina compacta</i>	3	2																		
<i>T. inflata</i>																				
<i>T. lobata</i>																				
<i>T. squamata</i>																				
<i>Virgulina fusiformis</i>																				
Unknown	6	4	4	3																
TOTALS	35	72	11	70	47	17	49	56	80	178	40	136	67	185	13	198	30	149	203	386
DEPTH IN METERS	20	19	17	20	34	37	29	25	23	18	15	14	16	16	14	15	10	10	15	4
VOL. IN ML.	10.0	17.4	10.5	19.2	16.9	17.7	15.3	18.6	19.4	14.7	14.0	16.6	11.2	13.0	17.4	18.9	12.1	13.4	16.6	14.0

TABLE 3—Continued

TRAVERSE STATIONS		3																			
		2	3	4	5	6	7	8	9	10	10'	11	12	13	1	1'	33	32	31	30	29
Ammonia beccarii	L	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	
Ammodendron cf. fluvialis																					
Bolivina variabilis																					
Buccella frigida																					
Cornuspira planorbis																					
Eggerella advena	100	50			17	2	44	11	64	34	50	24	31	26	4	4	3	3	.8	.3	
Elphidium clavatum		62	52	20	17	29	13	8	12	4	36	55	67	82	77	97	91	88	94	88	
E. pauciloculum		8	3	60	20	28	7	22	5	31	27	29	18	1	3	.2	.2	.1	2	2	
E. tisburyensis																					
E. varium		23	20	40	7	6	2	1	2	4	7	4	2	3	1	7	2	.6	.7	1	
Fissurina laevigata																					
Nonionella atlantica																					
Perozonoides lateralis																					
Pseudopolymorphinonovangioe																					
Quinqueloculina seminula																					
Q. seminula var. jugosa																					
Rhopax dentatiformis																					
R. nana																					
Trochammina compacta																					
T. inflata																					
T. lobata																					
T. squemata																					
Virgulina fusiformis																					
Unknown	50				2																
TOTALS	N	4	73	51	30	109	85	200	211	992	762	244	527	1002	591	1127	3415	680	2157	324	
DEPTH IN METERS	19	40	39	35	30	26	22	16	14	14	11	10	9	14	14	24	30	39	36	31	
VOL. IN ML.	25.1		7.1	12.6	8.1	7.2	9.8	7.5	11.0	11.5	10.8	9.6	12.4	4.9	8.6	17.6	14.6	17.5	14.4	18.4	





TABLE 3—Continued

TRAVERSE STATIONS	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Ammonia beccarii	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T
Ammoscalaria cf. fluviatilis																				
Bolivina variabilis																				
Buccella frigida	4	3	11	3	3	5	13	15	31	6	44	20	28	26	30	30	33	52	43	49
Cornuspira planorbis																				
Eggerella advena	3	.1	30	3	93	94	100	84	73	58	32	83	46	57	20	50	15	53	26	31
Ephidium clavatum	88	92	30	72		4	5	24	4	5	4	40	12	46	7	27	31	20	56	35
E. pauciloculum	3	2	.8			7	3													
E. tisburyensis																				
-E. varium																				
Fissurina laevigata	1	.4																		
Nonionella atlantica																				
Poreponides lateralis																				
Pseudopolymorphina novaeboracensis																				
Quinqueloculina seminula																				
Q. seminula var. jugosa																				
Rhopax dentatiniformis	10	2				5	4			2	2	.5								
R. nana												.8								
Trochammina compacta																				
T. inflata																				
T. lobata																				
T. squamata																				
Virgulina fusiformis	3	.1																		
Unknown	4	2	1			5	4	5	2	4	2	8	3	.7	1	3	2	6	3	1
TOTALS	368	990	10	254	24	14	37	12	73	173	48	125	49	191	270	260	112	127	82	440
DEPTH IN METERS	10	26	41	37	28	24	26	23	21	19	18	15	15	13	9	21	22	37	40	35
VOL. IN ML.	16.6	17.0	17.4	17.4	15.4	15.0	16.7	15.0	14.9	16.4	14.4	13.6	14.0	17.4	14.9	15.5	13.9	14.9	14.9	14.6





TABLE 3—Continued

TRAVERSE		3																			
STATIONS		105	104	104'	103	103a	103b	103c	102	102'	101	101a	101b	100	13	126	127	128	129	129'	130
Ammonia beccarii		L	T	T	L	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	L
Ammonocartio cf. fluviatilis																					
Bolivina variabilis																					
Buccella frigida		25	33	36	32	19	29	48	41	37	24	44	23	43	25	47	26	38	13	8	11
Cornuspira planorbis																					
Eggerella advena		73	12	17	6	40	3	54	14	20	3										
Ephidium clavatum		27	56	33	48	30	33	16	47	12	42	37	53	31	69	43	68	16	62	56	81
E. pauciloculum		1	7	10	13			8	3	5	6	3									
E. lieburgyensis																					
E. varium		4	6	10	12	3	6	4	7	4											
Fissurina laevigata				10	2		.5	1													
Nonionella affanica																					
Poroponidites lateralis																					
Pseudopolymerphina novaezooe																					
Quinqueloculina seminula																					
Q. seminula var. jugosa																					
Reophax dentatiformis		1			.5	4	.7	5	1												
R. nana				.9																	
Trochammina compacta																					
T. inflata																					
T. lobata																					
T. squamata																					
Virgulina fusiformis																					
Unknown		17	1	3	3	1	4	2	16	3	12	2									
TOTALS		11	6	165	10	191	25	270	19	213	16	176	7	276	19	245	16	443	13	651	32
DEPTH IN METERS		27	24	24	21	21	21	21	18	18	16	16	16	13	11	28	35	43	32	32	30
VOL. IN ML.		15.0	17.2	15.8	18.4	17.1	16.4	18.7	15.5	14.2	16.7	17.8	11.2	11.3	7.8	20.8	18.9	19.2	14.8	18.9	15.2





TABLE 3—Continued

TRAVERSE STATIONS	4				5															
	36	35	34	33	51	54	55	57	59	59'	50	16	17	18	19	19'	20	13		
<i>Ammonia beccarii</i>	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T	L	T
<i>Ammonia cf. fluviatilis</i>																				
<i>Bolivina variabilis</i>																				
<i>Buccella frigida</i>	7	8	7	7	4		14		3	4	2	4	1	2	8	1	2	5	1	1
<i>Cornuspira planorbis</i>									1											
<i>Eggerella advena</i>	1	1									3	2							6	1
<i>Elphidium clavatum</i>	70	85	100	90	75	93	43	100	73	73	63	69	74	79	90	90	98	97	98	93
<i>E. pauciloculum</i>			2	3	3			5	8	7	6	4	2	4	X		8	5	3	2
<i>E. flabryensis</i>								19	7	28	12				X					
<i>E. varium</i>	19	4	2		7		14		1	4	1	4								
<i>Fissurina laevigata</i>																				
<i>Nonionella atlantica</i>																				
<i>Porosponides lateralis</i>																				
<i>Pseudopolymorphina novaeboracensis</i>									1	4										
<i>Quinqueloculina seminula</i>									4	1	7	.6	1			X				
<i>Q. seminula</i> var. <i>jugosa</i>																				
<i>Reophax dentatiformis</i>	1	3																		
<i>R. nana</i>																				
<i>Trochammina compacta</i>																				
<i>T. inflata</i>									.4											
<i>T. lobata</i>																				
<i>T. squamata</i>			.1	.4	100	94	100	20	1		2	1								
<i>Virgulina fusiformis</i>	1	3	2	14	2				1	.4										
Unknown	67	336	6	996	65	8			269	86	97	282	62	163	4716	427	25171	681	10573	417
TOTALS																				
DEPTH IN METERS	19	17	16	14	12	37	37	25	3	3	15	12	5	7	3	3	4	10		
VOL. IN ML.	19.5	14.6	14.0	4.8	4.1	17.8	10.0	13.5	13.7	2.6	13.2	12.9	20.4	13.8	14.8	18.3	11.4			

TABLE 4.—*Grouping of seasonal stations into 13 grand stations.*

Grand stations	Station								
1.....	1								
2.....	2	33	32	84	96	126			
3.....	3	31	70	71	82	83	95	109	127
4.....	4	30	69	81	93	94	108	128	
5.....	5	29	68	80	92	107	129		
6.....	6	28	66	79	91	106	130		
7.....	7	27	65	78	90	105	131		
8.....	8	26	64	77	89	104	132		
9.....	9	25	63	76	88	103			
10.....	10	24	62	75	87	102	133		
11.....	11	23	61	74	86	101	134		
12.....	12	22	60	73	100	135			
13.....	13								

TABLE 5.—*Wilcoxon test on stations chosen at random in the E. advena zone in March 1962 and June 1962.*

## Total Living Population

Mar. 1962 .....	$n=5$ $m=5$	$R_m=27$	June 1962 .....	$n=5$ $m=5$	$R_m=23$
-----------------	----------------	----------	-----------------	----------------	----------

Numbers of Living *E. clavatum*

Mar. 1962 .....	$n=5$ $m=5$	$R_m=24$	June 1962 .....	$n=5$ $m=5$	$R_m=22$
-----------------	----------------	----------	-----------------	----------------	----------

Numbers of Living *B. frigida*

Mar. 1962 .....	$n=5$ $m=5$	$R_m=25$	June 1962 .....	$n=5$ $m=5$	$R_m=20$
-----------------	----------------	----------	-----------------	----------------	----------

Numbers of Living *E. advena*

Mar. 1962 .....	$n=5$ $m=5$	$R_m=26$	June 1962 .....	$n=5$ $m=5$	$R_m=25$
-----------------	----------------	----------	-----------------	----------------	----------



TABLE 6.—*Wilcoxon test on number of living E. advena in E. advena zone.*

June 1961 . . . . .	$m = 8$	$R_m = 48^*$	Jan. 1962 . . . . .	$m = 8$	$R_m = 93$
Oct. 1961 † . . . . .	$n = 8$		Mar. 1962 . . . . .	$n = 10$	
June 1961 . . . . .	$n = 8$	$R_m = 58$	Jan. 1962 . . . . .	$m = 8$	$R_m = 82$
Jan. 1962 . . . . .	$m = 8$		June 1962 . . . . .	$n = 10$	
June 1961 . . . . .	$m = 8$	$R_m = 68$	Jan. 1962 † . . . . .	$n = 8$	$R_m = 36^*$
Mar. 1962 . . . . .	$n = 10$		Sept. 1962 . . . . .	$m = 7$	
June 1961 . . . . .	$m = 8$	$R_m = 65$	Jan. 1962 † . . . . .	$n = 8$	$R_m = 34^*$
June 1962 . . . . .	$n = 10$		Nov. 1962 . . . . .	$m = 7$	
June 1961 . . . . .	$n = 8$	$R_m = 59$	Mar. 1962 . . . . .	$n = 10$	$R_m = 87$
Sept. 1962 . . . . .	$m = 7$		June 1962 . . . . .	$m = 10$	
June 1961 . . . . .	$n = 8$	$R_m = 63$	Mar. 1962 . . . . .	$n = 10$	$R_m = 45$
Nov. 1962 . . . . .	$m = 7$		Sept. 1962 . . . . .	$m = 7$	
Oct. 1961 . . . . .	$n = 8$	$R_m = 85$	Mar. 1962 † . . . . .	$n = 10$	$R_m = 41^*$
Jan. 1962 . . . . .	$m = 8$		Nov. 1962 . . . . .	$m = 7$	
Oct. 1961 † . . . . .	$m = 8$	$R_m = 110^*$	June 1962 † . . . . .	$n = 10$	$R_m = 38^*$
Mar. 1962 . . . . .	$n = 10$		Sept. 1962 . . . . .	$m = 7$	
Oct. 1961 † . . . . .	$m = 8$	$R_m = 102^*$	June 1962 † . . . . .	$n = 10$	$R_m = 32^*$
June 1962 . . . . .	$n = 10$		Nov. 1962 . . . . .	$m = 7$	
Oct. 1961 † . . . . .	$n = 8$	$R_m = 30^*$	Sept. 1962 . . . . .	$n = 7$	$R_m = 52$
Sept. 1962 . . . . .	$m = 7$		Nov. 1962 . . . . .	$m = 7$	
Oct. 1961 † . . . . .	$n = 8$	$R_m = 28^*$			
Nov. 1962 . . . . .	$m = 7$				

\* Significant at the 95 percent level.

† Greater number of living individuals.

TABLE 7.—*Wilcoxon test on numbers of living E. clavatum in E. advena zone.*

June 1962 † . . . . .	$n = 10$	$R_m = 32^*$	June 1962 † . . . . .	$n = 10$	$R_m = 66^*$
Sept. 1962 . . . . .	$m = 7$		Mar. 1962 . . . . .	$m = 10$	
June 1962 † . . . . .	$n = 10$	$R_m = 39^*$	Nov. 1962 . . . . .	$m = 7$	$R_m = 64$
Nov. 1962 . . . . .	$m = 7$		Jan. 1962 . . . . .	$n = 8$	

\* Significant at the 95 percent level.

† Greater number of living individuals.



TABLE 8.—*Wilcoxon test on numbers of living B. frigida in E. advena zone.*

June 1961 . . . . .	$n = 8$	$R_m = 61$	June 1962 † . . . . .	$n = 10$	$R_m = 40^*$
Oct. 1961 . . . . .	$m = 8$		Sept. 1962 . . . . .	$m = 10$	
June 1961 . . . . .	$n = 8$	$R_m = 55$	June 1962 . . . . .	$n = 10$	$R_m = 97$
Jan. 1962 . . . . .	$m = 8$		Mar. 1962 . . . . .	$m = 10$	
June 1961 . . . . .	$m = 8$	$R_m = 73$	June 1962 . . . . .	$n = 10$	$R_m = 62$
Mar. 1962 . . . . .	$n = 10$		Jan. 1962 . . . . .	$m = 8$	
June 1961 . . . . .	$m = 8$	$R_m = 64$	June 1962 . . . . .	$n = 10$	$R_m = 57$
June 1962 . . . . .	$n = 10$		Oct. 1961 . . . . .	$m = 8$	
June 1961 . . . . .	$n = 8$	$R_m = 52$	June 1962 † . . . . .	$n = 10$	$R_m = 42^*$
Sept. 1962 . . . . .	$m = 7$		Nov. 1962 . . . . .	$m = 7$	

\* Significant at the 95 percent level.

† Greater number of living individuals.

TABLE 9.—*Wilcoxon test on numbers of living individuals of all species in the E. advena zone.*

June 1961 . . . . .	$n = 8$	$R_m = 60$	Oct. 1961 . . . . .	$m = 8$	$R_m = 81$
Jan. 1962 . . . . .	$m = 8$		June 1962 . . . . .	$n = 10$	
June 1961 . . . . .	$m = 8$	$R_m = 69$	June 1961 . . . . .	$m = 8$	$R_m = 60$
March 1962 . . . . .	$n = 10$		June 1962 . . . . .	$n = 10$	
June 1961 . . . . .	$n = 8$	$R_m = 53$	June 1962 † . . . . .	$n = 10$	$R_m = 73^*$
Sept. 1962 . . . . .	$m = 7$		March 1962 . . . . .	$m = 10$	
June 1961 . . . . .	$m = 8$	$R_m = 53$	June 1962 † . . . . .	$n = 10$	$R_m = 32^*$
Oct. 1961 . . . . .	$n = 8$		Sept. 1962 . . . . .	$m = 7$	
Oct. 1961 † . . . . .	$n = 8$	$R_m = 51^*$	June 1962 . . . . .	$n = 10$	$R_m = 54$
Jan. 1962 . . . . .	$m = 8$		Jan. 1962 . . . . .	$m = 8$	

\* Significant at the 95 percent level.

† Greater number of living individuals.

TABLE 10.—Numbers of individuals in samples from short cores.

TRAVERSE STATIONS	3																			
	74	74a	101	101a	101b	103	103a	103b	103c	107	107a	107b	107c	107d	107e	107f	107g	107h	107i	107j
Ammonia beccarii	L	T	T	L	T	T	L	T	T	L	T	T	L	T	T	L	T	T	L	T
Ammonicalaria cf. fluviatilis																				
Bolivina variabilis			1	1																
Buccella frigida	40	113	45	202	6	65	1	70	6	71	7	56	12	111	7	51	7	41		
Cornuspira planorbis																				
Eggerella advena	8	17	6	9				11		20	27	5	8		1	1	2	7	10	13
Elphidium clavatum	16	248	60	421	9	348	11	535	21	415	6	90	3	113	7	123	5	121	2	86
E. pauciloculum	3	5	1	20	10	6		4				2	8	1	13	1	5	2	3	4
E. tieburysensis	1																			
E. varium	10	41	3	44	1	15		31	2	23	1	12	1	20	8	3	5	1	6	3
Fissurina laevigata			2	3	1															
Nonionella atlantica																				
Perozonoides lateralis																				
Pseudopolymorphina novargioae																				
Quinqueloculina seminula																				
Q. seminula var. jugosa																				
Reophax dentatiformis	2	9	1	3																
R. nana																				
Trochammina compacta																				
T. inflata																				
T. lobata																				
T. squamata	1																			
Virgulina fusiformis																				
Unknown	5	12	2	6	3	1	5	3	7	1	2	1	5	3	7	2	4	1	2	4
TOTALS	82	440	170	688	16	493	651	13	520	37	191	25	270	23	16	176	25	140	133	192
DEPTH IN METERS	15	15	16	16	16	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21
VOL. IN ML.	13.6	14.0	18.2	17.8	11.2	18.4	17.1	18.4	18.7	13.5	14.4	14.7	18.9	16.4	18.1	18.2	19.9			

TABLE 11.—*Statistical parameters for the sediments in L.I.S.*

Station No.	Md $\phi$	M $\phi$	$\sigma\phi$	$\alpha\phi$	Niggli's classification
1a.....	0.8	0.8	0.5	0.00	sand
96a.....	1.5	2.6	1.8	0.61	silty sand
95a.....	1.4	3.4	3.0	0.66	sand
4a.....	5.2	5.3	3.3	0.03	clayey sand
5a.....	6.6	5.6	3.0	-0.33	clayey silt
6a.....	6.8	6.7	1.9	-0.05	clayey silt
7a.....	6.7	6.6	2.0	0.00	clayey silt
8a.....	5.9	6.1	2.5	0.08	clayey silt
9a.....	6.6	6.6	2.0	0.00	clayey silt
10a.....	6.7	6.5	2.1	-0.09	clayey silt
11a.....	6.5	6.4	2.2	-0.04	silt
12a.....	6.4	6.3	2.3	-0.04	clayey silt
13a.....	0.8	0.3	1.1	-0.45	sand
34a.....	5.9	6.4	2.2	0.23	silt
35a.....	4.4	5.1	2.2	0.32	silty sand
36a.....	4.9	5.9	2.1	0.48	silt
37a.....	4.8	6.0	2.2	0.54	silt
38a.....	4.4	5.9	2.4	0.62	silty sand
39a.....	4.3	5.6	2.4	0.54	silty sand
40a.....	4.1	5.2	2.0	0.55	silty sand
41a.....	4.3	5.4	2.4	0.46	silty sand
42a.....	3.9	5.2	2.0	0.65	silty sand
44a.....	4.8	5.4	2.2	0.27	silty sand
45a.....	4.3	5.6	2.4	0.54	silty sand
46a.....	5.3	6.0	2.6	0.27	silty sand
47a.....	5.0	6.1	2.4	0.46	silty sand
48a.....	5.3	6.3	2.3	0.44	silty sand
51a.....	-0.1	-0.1	0.9	0.00	sand
54a.....	0.6	-0.1	1.4	-0.50	sand
55a.....	3.3	3.6	3.2	0.09	silty sand
56.....	0.6	-0.6	2.0	-0.60	pebble sand
57.....	4.8	4.9	3.6	0.03	silty sand
58.....	1.5	1.6	0.4	0.25	sand
114a.....	7.2	6.9	1.8	-0.17	clayey silt
116a.....	2.3	4.4	2.8	0.75	silty sand
117a.....	2.4	5.0	3.2	0.81	silty sand
118a.....	2.4	5.0	3.2	0.81	silty sand
119a.....	7.2	6.4	2.2	-0.36	clayey silt
120a.....	6.6	6.3	2.5	-0.12	clayey silt
121a.....	6.8	5.6	3.2	-0.38	clayey silt
122a.....	6.9	6.7	2.1	-0.10	clayey silt
123a.....	3.2	5.1	3.2	0.59	silty sand
124a.....	6.0	6.0	2.8	0.00	clayey silt

TABLE 11—(continued)

Station No.	Md $\phi$	M $\phi$	$\sigma\phi$	$\alpha\phi$	Niggli's classification
110a.....	1.9	4.1	3.9	0.56	silty sand
111a.....	1.3	2.4	1.8	0.61	sand
97a.....	5.0	5.4	2.8	0.14	silty sand
80a.....	0.9	1.9	2.7	0.37	sand
14a.....	1.0	0.8	2.0	-0.10	sand
15a.....	6.8	6.9	1.7	0.06	clayey silt
16a.....	2.6	3.8	2.4	0.50	silty sand
18a.....	4.0	1.8	4.2	-0.50	silty sand
19a.....	0.7	-0.4	2.8	-0.39	pebble sand
20a.....	3.5	3.0	5.2	-0.10	silty sand
50a.....	2.2	2.0	1.2	-0.17	sand
59a.....	5.8	6.5	2.1	0.33	silt
98.....	6.2	6.2	2.3	0.00	silt
112a.....	6.3	5.6	3.0	-0.23	clayey sand
113a.....	7.0	5.7	3.0	-0.43	clayey silt
125a.....	-1.8	-2.2	2.6	-0.15	pebble sand



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## EXPLANATION OF PLATES

### PLATE 1

- Fig. 1. *Reophax dentaliniformis* Brady. U.S.N.M. 641393.  $\times 65$   
 Fig. 2. *Reophax nana* Rhumbler. U.S.N.M. 641394.  $\times 215$ .  
 Fig. 3. *Ammoscalaria* cf. *fluvialis* Parker. U.S.N.M. 641395.  $\times 65$ .  
 Fig. 4. *Eggerella advena* (Cushman). U.S.N.M. 641396.  $\times 150$ .  
 Fig. 5. *Eggerella advena* (Cushman). U.S.N.M. 641397.  $\times 150$ .  
 Fig. 6. *Quinqueloculina seminulum* (Linné). U.S.N.M. 641398.  $\times 150$ .  
 Fig. 7. *Quinqueloculina seminulum* var. *jugosa* Cushman. U.S.N.M. 641399.  
 $\times 93$ .  
 Fig. 8. *Cornuspira planorbis* Schultze. U.S.N.M. 641400.  $\times 150$ .  
 Fig. 9. *Trochammina inflata* (Montagu). U.S.N.M. 641401. a, Dorsal view;  
 b, ventral view.  $\times 150$ .  
 Fig. 10. *Trochammina lobata* Cushman. U.S.N.M. 641402. Dorsal view.  $\times 280$ .

### PLATE 2

- Fig. 1. *Trochammina lobata* Cushman. U.S.N.M. 641402. Ventral view.  $\times 280$ .  
 Fig. 2. *Trochammina squamata* Parker and Jones. U.S.N.M. 641403. a, Dorsal  
 view; b, ventral view.  $\times 150$ .  
 Fig. 3. *Fissurina laevigata* Reuss. U.S.N.M. 641404.  $\times 150$ .  
 Fig. 4. *Pseudopolymorphina novangliae* (Cushman). U.S.N.M. 641405.  $\times 33$ .  
 Fig. 5. *Nonionella atlantica* Cushman. U.S.N.M. 641406. a, Dorsal view; b,  
 ventral view.  $\times 150$ .  
 Fig. 6. *Elphidium clavatum* Cushman. U.S.N.M. 641407.  $\times 150$ .  
 Fig. 7. *Elphidium clavatum* Cushman. U.S.N.M. 641408.  $\times 150$ .

### PLATE 3

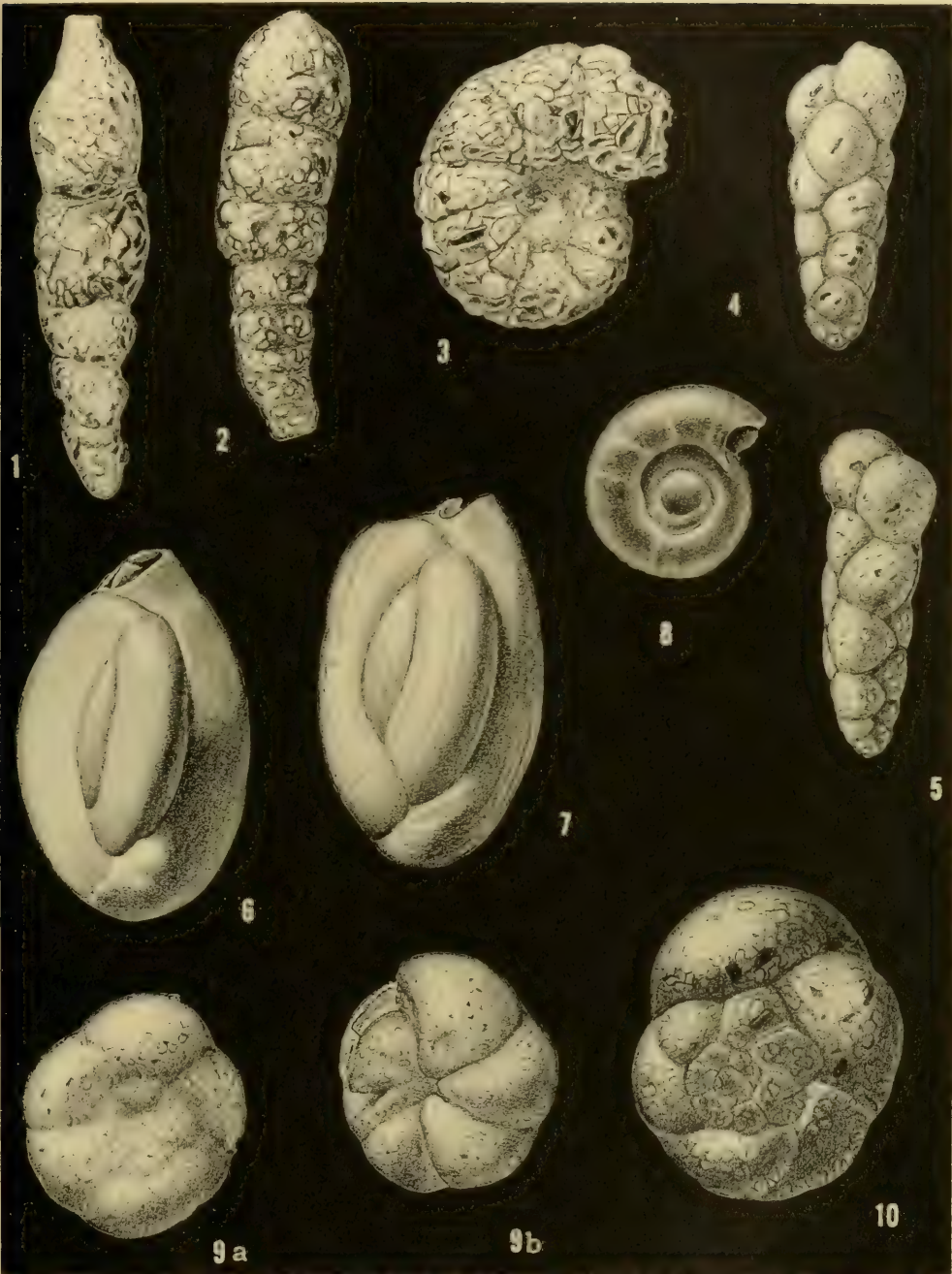
- Fig. 1. *Elphidium clavatum* Cushman. U.S.N.M. 641409.  $\times 150$ .  
 Fig. 2. *Elphidium clavatum* Cushman. U.S.N.M. 641410.  $\times 150$ .  
 Fig. 3. *Elphidium pauciloculum* (Cushman). U.S.N.M. 641411.  $\times 150$ .  
 Fig. 4. *Elphidium tisburyense* (Butcher). U.S.N.M. 641412.  $\times 150$ .  
 Fig. 5. *Elphidium varium* Buzas. U.S.N.M. 641413.  $\times 93$ .  
 Fig. 6. *Bolivina variabilis* (Williamson). U.S.N.M. 641414.  $\times 280$ .  
 Fig. 7. *Virgulina fusiformis* (Williamson). U.S.N.M. 641415.  $\times 214$ .

### PLATE 4

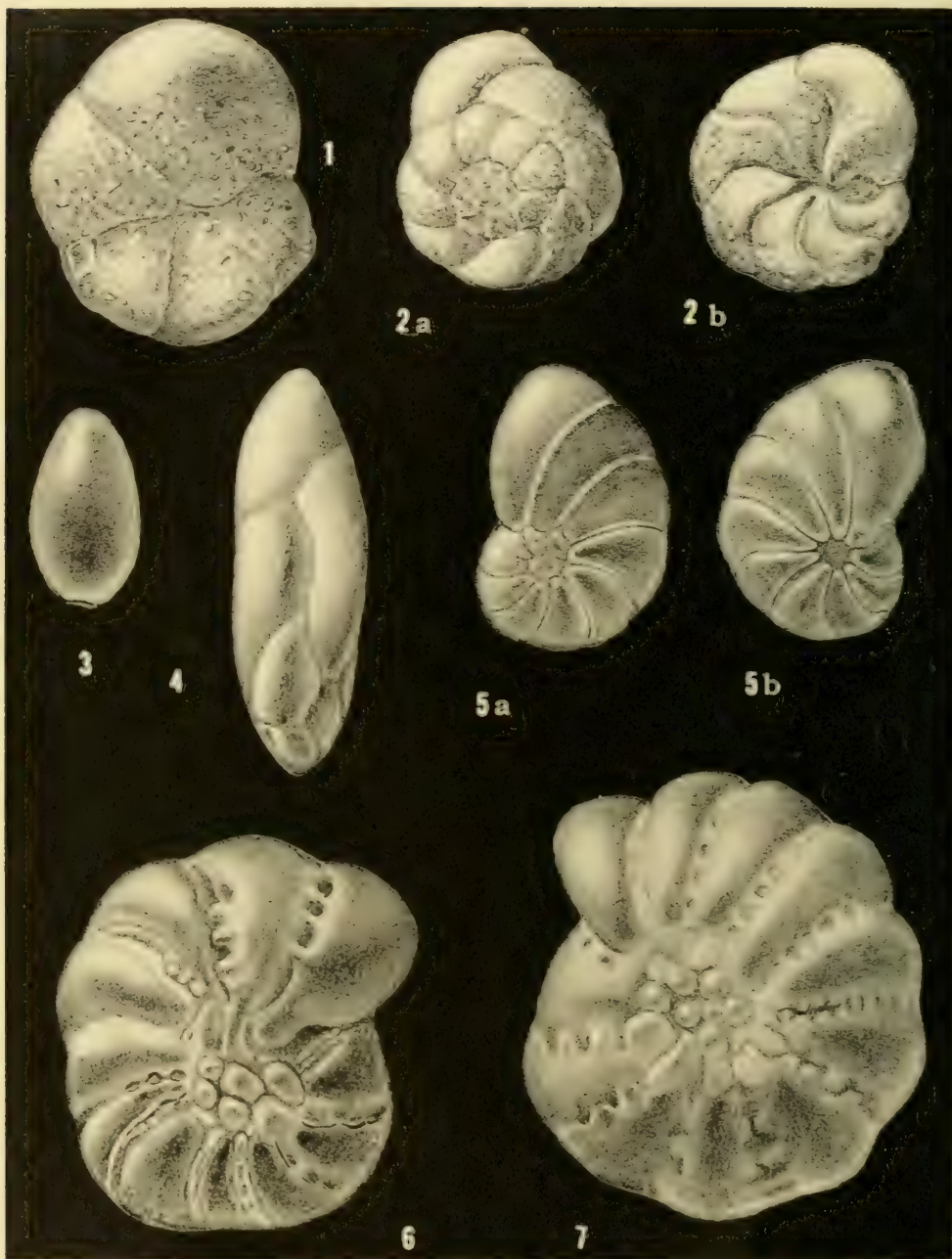
- Fig. 1. *Ammonia beccarii* (Linné). U.S.N.M. 641416. a, Dorsal view; b, ven-  
 tral view.  $\times 150$ .  
 Fig. 2. *Buccella frigida* (Cushman). U.S.N.M. 641417. a, Dorsal view; b, ven-  
 tral view.  $\times 150$ .  
 Fig. 3. *Buccella frigida* (Cushman). U.S.N.M. 641418. a, Dorsal view; b, ven-  
 tral view.  $\times 150$ .  
 Fig. 4. *Poroeponides lateralis* (Terquem). U.S.N.M. 641419.  $\times 93$ .





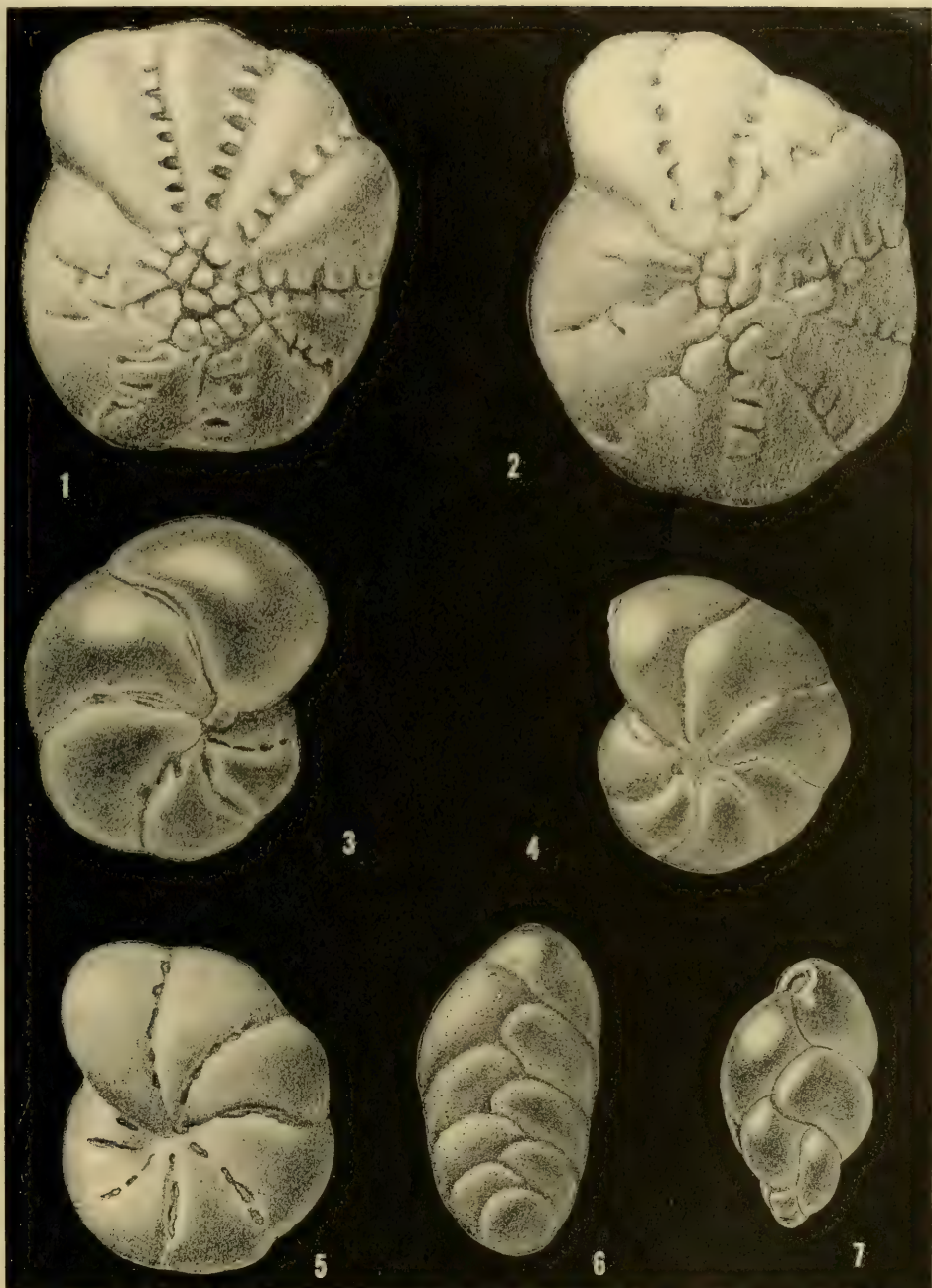


FORAMINIFERA FROM LONG ISLAND SOUND  
(SEE EXPLANATION OF PLATES AT END OF TEXT.)



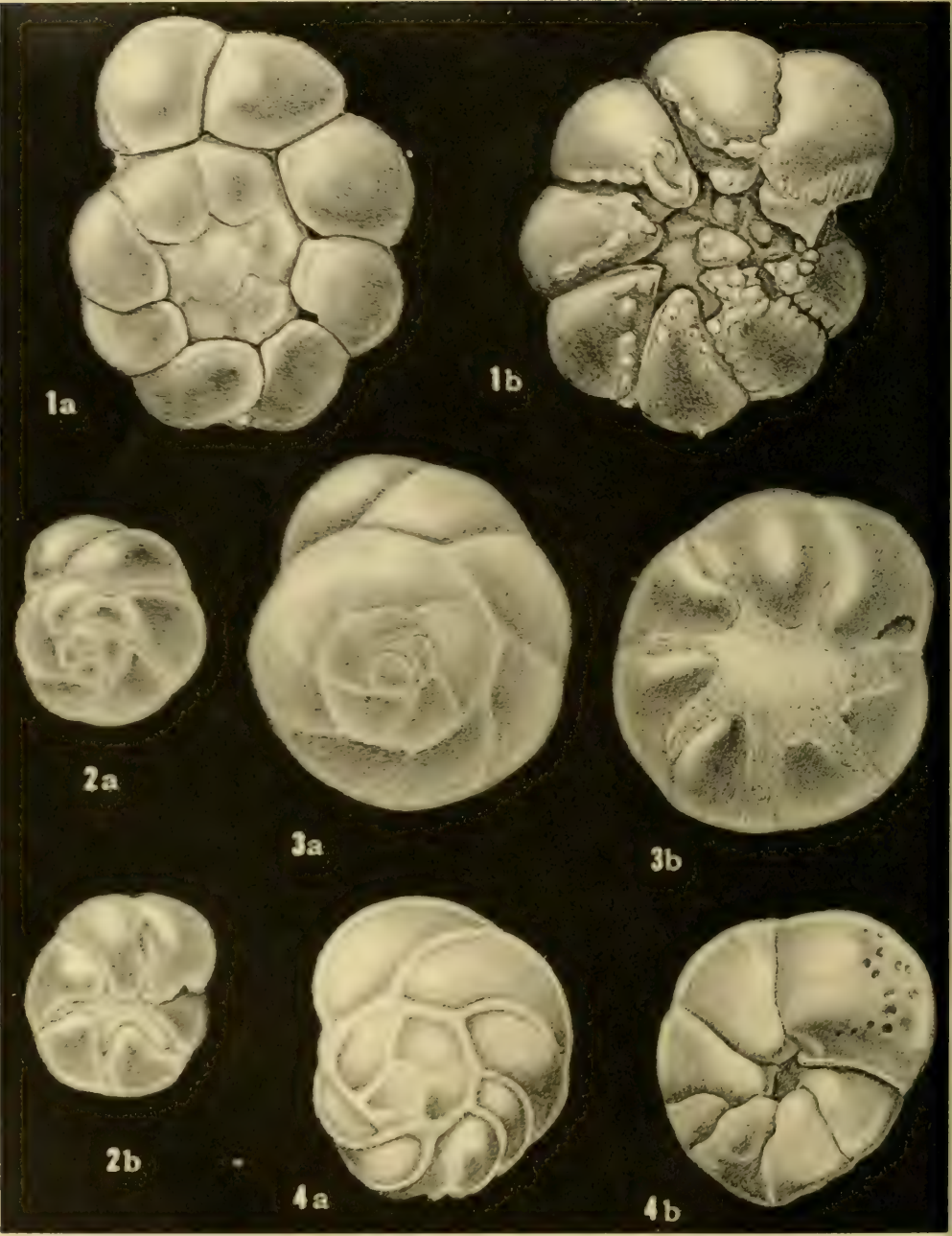
FORAMINIFERA FROM LONG ISLAND SOUND  
(SEE EXPLANATION OF PLATES AT END OF TEXT.)





FORAMINIFERA FROM LONG ISLAND SOUND  
(SEE EXPLANATION OF PLATES AT END OF TEXT.)





FORAMINIFERA FROM LONG ISLAND SOUND  
(SEE EXPLANATION OF PLATES AT END OF TEXT.)





SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 149, NUMBER 2

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Charles D. and Mary Vaux Walcott  
Research Fund

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A STUDY OF THE EARLY TERTIARY  
CONDYLARTHAN MAMMAL  
MENISCOTHERIUM

(WITH 11 PLATES)

By

C. LEWIS GAZIN

Curator, Division of Vertebrate Paleontology  
U. S. National Museum  
Smithsonian Institution



(PUBLICATION 4605)

CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION  
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## CONTENTS

	Page
Introduction .....	1
Acknowledgments .....	2
History of investigation .....	3
Geographic and geologic occurrence .....	9
Environment .....	13
Classification .....	20
The skeleton of <i>Meniscotherium</i> , with notes on <i>Phenacodus</i> , <i>Hyopsodus</i> , and other condylarths .....	22
Skull .....	22
Endocranial cast .....	35
Mandible .....	39
Dentition .....	41
Vertebrae .....	45
Scapula .....	50
Humerus .....	51
Radius .....	53
Ulna .....	54
Manus .....	55
Pelvic girdle .....	64
Femur .....	65
Tibia .....	67
Fibula .....	69
Pes .....	70
Summary of relationships .....	81
References .....	90
Explanation of plates .....	96



# ILLUSTRATIONS

## PLATES

(All plates following p. 98.)

1. *Meniscotherium* skull from the early Eocene of Wyoming.
2. *Meniscotherium* skull from the early Eocene of Wyoming.
3. *Meniscotherium* from the early Eocene of Wyoming.
4. *Meniscotherium* type specimens.
5. *Meniscotherium* dentitions from the early Eocene of Wyoming.
6. *Meniscotherium* humerus and scapula from the early Eocene of Wyoming.
7. *Meniscotherium* fore limb and foot material from the early Eocene.
8. *Meniscotherium* femur and patella from the early Eocene of Wyoming.
9. *Meniscotherium* tibia and fibula from the early Eocene of Wyoming.
10. *Meniscotherium* pedes from the early Eocene.
11. Restoration of *Meniscotherium*.

## TEXT FIGURES

	Page
1. Skeleton of <i>Meniscotherium chamense</i> Cope.....	20
2. Endocranial cast of <i>Meniscotherium chamense</i> Cope .....	36
3. Endocast of skull of <i>Meniscotherium robustum</i> Thorpe .....	36
4. Endocast of cranial roof of <i>Meniscotherium robustum</i> Thorpe .....	36
5. Cervical and anterior dorsal vertebrae of <i>Meniscotherium chamense</i> Cope .....	46
6. Cervical and anterior dorsal vertebrae of <i>Meniscotherium robustum</i> Thorpe .....	47
7. Lumbar and posterior dorsal vertebrae of <i>Meniscotherium chamense</i> Cope .....	48
8. Lumbar and sacral vertebrae, and pelvic girdle of <i>Meniscotherium</i> <i>robustum</i> Thorpe .....	49
9. Caudal vertebrae of <i>Meniscotherium robustum</i> Thorpe .....	50

## CHART

	Page
1. Distribution of species of <i>Meniscotherium</i> by horizon in various basins, or areas within basins of deposition .....	12

Charles D. and Mary Vaux Walcott Research Fund

A STUDY OF THE EARLY TERTIARY  
CONDYLARTHAN MAMMAL  
MENISCOTHERIUM <sup>1</sup>

By C. LEWIS GAZIN

*Curator, Division of Vertebrate Paleontology  
U. S. National Museum  
Smithsonian Institution*

(WITH 11 PLATES)

INTRODUCTION

The genus *Meniscotherium*, although first described nearly ninety years ago, has heretofore received but little systematic or detailed study. Exception, however, must be made of E. D. Cope's rather thorough treatment of the very limited material available to him by 1884. There are, nevertheless, rather numerous references to *Meniscotherium* in the literature of vertebrate paleontology, and these serve not only to illustrate the wide interest that was early aroused, but also to direct attention to the strikingly diverse opinions held as to its relationships.

*Meniscotherium* is a condylarthran mammal characterized by primitive flat-nailed unguiculate or subungulate feet with essentially a serial arrangement of the carpals and tarsals, but associated with precociously selenodont teeth. Nearly all the known material is early Eocene or Wasatchian in age, although one, or possible two, Paleocene occurrences have been recorded. Its geographic distribution in Wasatchian time is the San Juan Basin of northwestern New Mexico, the Green River Basin and adjacent areas of southwestern Wyoming, and the valley of the Colorado River in western Colorado.

Investigation of the morphology and relationships of this highly interesting form was inspired by the abundant, unusually well-preserved remains encountered by Smithsonian Institution field parties

---

<sup>1</sup> Study of early Tertiary mammals is currently aided by a grant from the National Science Foundation.

while collecting in the Knight and New Fork members of the Wasatch formation in southwestern Wyoming during various field seasons since 1948.

#### ACKNOWLEDGMENTS

Although the present study is based principally on the *Meniscotherium* remains in the U. S. National Museum, the work has been advanced immeasurably through the courtesies extended by various universities and other museums in permitting access to related comparative materials and in lending certain types and representative specimens for further study in Washington.

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Dr. George G. Simpson early expressed an interest in making a study of *Meniscotherium* (see Gazin, 1952, p. 61) as a result of his extensive collection for the American Museum of materials representing the San Juan Basin population. Since moving to Cambridge, however, he has indicated with regret the improbability of his carrying out this study in the near future. His deferring to my interest in this undertaking is much appreciated.

The incomparable pencil drawings reproduced in the accompanying plates (except pl. 11), as well as the text figures, were prepared by Lawrence B. Isham, staff illustrator for the Department of Paleobiology in the U. S. National Museum.

#### HISTORY OF INVESTIGATION

*Discovery and description.*—*Meniscotherium* was first described by Cope in 1874. The specimen on which the type species, *M. chamense*, was based is a right maxillary fragment exhibiting the molars and outer wall of the last premolar, found that summer in the San Juan Basin of New Mexico in the region between Canyon Largo and Gallina River. No new material was reported until 1881 (b) when Cope described a left maxilla with three molars and three premolars and an associated lower jaw fragment with two teeth as representing a new and somewhat larger species, *M. terraerubrae*. Description of this material was included with that of Torrejonian Paleocene forms from the "Lowest Eocene beds of New Mexico." Cope stated (p. 495) that the new *Meniscotherium* specimens found by D. Baldwin were from "the red Eocene beds in northwestern New Mexico, from the true Wasatch horizon, or higher than that which produced other species here described." Nevertheless, there must have been some doubt in his mind as to the horizon represented because elsewhere on the same page, in discussing the fauna of the beds he thought were quite possibly the Puerco formation, he stated that he had now added the genera *Hyracotherium* and *Meniscotherium*.

A third and smallest species of *Meniscotherium*, *M. tapiacitis*, was described by Cope late in 1882(f). At this time there was apparently no confusion with the Paleocene. *M. tapiacitis* is stated to have been collected "by D. Baldwin from beds of probably lowest Wasatch age in New Mexico."

Marsh's description of *Hyracops socialis* in 1892 was based on skull and foot material collected by David Baldwin in 1878. While Marsh's report on meniscotheriid remains from the Wasatchian of New Mexico was much later than Cope's, Baldwin's collecting for Marsh evidently preceded his employment by Cope. The specimens according to Thorpe (1934) came from the head of Gabilan Canyon, a branch of Canyon Largo in the San Juan Basin. The distinction which Marsh made between *Hyracops* and *Meniscotherium* was based essentially on the molariform appearance of the last premolar and possession of an extra sacral vertebra, features that Thorpe has since shown to be invalid in that the premolar described belonged to the



deciduous series and the number of vertebrae in the sacrum is consistent with *Meniscotherium*.

Later reports of discovery and description of new materials include an announcement by Granger in 1910 of the finding of *Meniscotherium* in the Lost Cabin beds of the Wind River Basin. He regarded this as the first record outside of the Wasatchian of New Mexico, although in 1915 he noted materials collected from the Wind River Basin as early as 1896. He was evidently not aware of the listing of *Meniscotherium chamense* by Clarence King in 1878 in the fauna for his Vermilion Creek group in Wyoming. The faunal lists in King's work, according to Hay (Bibliography of 1902), were probably furnished by Marsh, and it follows that the material referred to may well have been the Knight skull collected for Marsh in 1875 and that much later became the type of *Meniscotherium robustum* Thorpe. In 1915 Granger reviewed the characters and distribution of the genus *Meniscotherium*, revising the species to include Cope's *M. terraerubrae* as a subspecies of *M. chamense*, and adding the new species *Meniscotherium*(?) *priscum* from the Clark Fork Paleocene of northwestern Wyoming. Regarding it as a second species of Paleocene age, Russell (1929) described *Meniscotherium semicinctatum* from a locality in Alberta, Canada. The age is questioned but thought to be Clarkforkian because of the association of *Ptilodus* with forms of Wasatchian aspect.

It was not until 1934 that the material of *Meniscotherium* referred to above as having come from southwestern Wyoming in 1875 was described. Though rather poorly preserved, the specimen includes most of the skull and lower jaws. It was collected for Marsh by William Cleburne in a railroad cut near Aspen in Uinta County. Thorpe made this the type of the new species *Meniscotherium robustum*, a form that I (1952) found to be characteristic of the La Barge fauna from the Knight beds in the Green River Basin. In this 1934 paper Thorpe also gave the evidence for suppressing Marsh's name "*Hyracops*," which in any case had long been regarded as a synonym of *Meniscotherium*.

The known distribution of *Meniscotherium* both geographically and geologically was summarized by Van Houten in 1945, and certain suggestions as to its ecology were presented by Simpson in 1948 as a part of his discussion of the occurrence of *Meniscotherium* in the San José beds of New Mexico. In a study of the Knight faunas of southwestern Wyoming in 1952 I summarized briefly the history of *Meniscotherium* discoveries and called attention to the abundant,

well-preserved material encountered at certain localities. Peculiarities of distribution attributed to ecology within the southwestern Wyoming area were cited in 1959 and 1962.

*Relationships.*—In reviewing the hypotheses and conclusions as to *Meniscotherium* relationships it may be noted that in Cope's original description of *Meniscotherium chamense* (1874) he did not make an ordinal assignment but regarded the new form as presenting "a curious combination in structure of its molars of the character of *Palaeosyops*, *Hyopotamus*, and *Hipposyus*." He probably did not intend to imply, in citing the latter, any suggestion of primate relationships because at that time he regarded *Hipposyus* (= *Notharctus*) as a primitive horse with *Orohippus* as a synonym. In repeating his description of *Meniscotherium* in 1877, however, Cope listed it in first place among the Perissodactyla, immediately preceding "*Orotherium*" (= *Orohippus*) in which he had included certain species of *Hyracotherium*.

In a further development of a systematic arrangement of perissodactyls in 1881(a) the genera were divided among 10 families, and *Meniscotherium* was listed in the Chalicotheriidae along with certain Eocene titanotheres, Old World *Propalaeotherium* and *Rhagatherium*, as well as the chalicotheres proper. The families as outlined were distinguished essentially by patterns of crescents and cross-crests in upper and lower molars, the extent to which the premolars resemble the molars, and the number of toes. The feet of *Meniscotherium*, however, were not known at that time, so that conclusions as to relationships were based entirely on the dentition, presumably the upper molars only, as displayed in the type of *M. chamense*.

Evidently the newer material cited later in 1881(b) included certain limb elements, possibly associated with tooth material, because in the spring of 1882(a) Cope stated that the astragalus and humerus had the characters of those of *Phenacodus*. As a result he concluded that *Meniscotherium*, for which he proposed the new family rank Meniscotheriidae, belonged with the Phenacodontidae (including the periptychids) in the recently (1881c) erected suborder, Condylarthra, under the Perissodactyla. Meniscotheriidae was distinguished by a lophodont dentition, "with external and internal crescents and deep valleys." Further concern about the foot structure of *Phenacodus* led Cope a couple of months later (1882c) to remove the Condylarthra from the Perissodactyla, and place them along with the Proboscidea in the new order or suborder Taxeopoda, having equal rank with Hyracoidea, Amblypoda, Perissodactyla, and

Artiodactyla under the Ungulata. The basis of this classification was presented in greater detail in his "Classification of the Ungulate Mammalia," published the same year (1882e). It is also this year (1882d) that Cope reported receiving foot material of *Periptychus* which led him to remove the periptychids from the Phenacodontidae as a third family of the Condylarthra.

Cope's ideas on condylarth classification were essentially crystallized by the time of his "Tertiary Vertebrata" (1884b) with little change since 1882, except that he had withdrawn the Proboscidea from the Taxeopoda, but included the Hyracoidea, suggesting a closer relationship of the latter to the Condylarthra. His treatment of *Meniscotherium* in this volume covers in detail the osteology of the skeleton, so far as it was then known, and is the most thorough to date. The more generalized part of this description appeared in a review of the Condylarthra in the American Naturalist for 1884(a) and as a separate brochure.

Later statements by Cope concerning *Meniscotherium* were essentially in defense of his interpretation of its relationships. In 1886 he criticized Schlosser (1886) for including *Meniscotherium* in the Perissodactyla instead of the Condylarthra, in placing more emphasis on teeth than on feet. In the following year he disputed Pavlov's (1887) assumption that *Meniscotherium* belongs to the Propalaeotheriidae and is perhaps a synonym of *Propalaeotherium*, reiterating his belief in the importance of foot structure in interpretations of relationship among ungulates.

Cope's briefly held interpretation (1881a) that *Meniscotherium* belonged with the chalicotheres was evidently favored by Schlosser (1886), as he regarded *Meniscotherium* as a perissodactyl with primitive feet and with teeth strikingly like *Chalicotherium*. This relationship is unquestioned in 1902, as evident from the statement, "Die Chalicotheriiden endlich stammen zwar aus Nordamerika—*Meniscotherium*—. . ." Although Zittel in 1893 followed more closely Cope's arrangement with the Meniscotheriidae, Phenacodontidae, etc., in the suborder Condylarthra, but under the Ungulata rather than Cope's Taxeopoda, Schlosser in a revision of Zittel's texts in 1911 and 1923 still regarded *Meniscotherium* as the ancestor or near the ancestry of the chalicotheres.

No doubt Schlosser was early confirmed in his conclusions regarding chalicothere affinity by Osborn (1891), who felt that the teeth of *Meniscotherium* pointed strongly toward a relationship with the chalicotheres, but awaited information on the structure of the feet.



He was evidently not satisfied with the fragmentary evidence of foot structure available to Cope. Moreover, upon description of the feet of the meniscotheriid "*Hyracops socialis*" by Marsh (1892), Osborn (1892a), in spite of the many discrepancies, concluded that the structures displayed supported a chalicothere relationship, appealing to the time interval separating the known materials of the two groups. It seems evident, however, that he nevertheless retained the Meniscotheriidae in the Condylarthra at that time because in 1895 (with Charles Earle) he suggested that this family as well as the Peripitychidae should probably be removed from the order, although no different allocation was made. By 1907 Osborn's conviction concerning chalicothere relationship seems to have weakened because, while in one place (p. 87) he states that, "It is thus suggested that *Meniscotherium* may be related to *Chalicotherium*"; on another page (184) appears, "However recent observations tend to show that these resemblances [in teeth] are not indicative of genetic relationship but that the chalicotheres have more probably been derived from lower Eocene titanotheres."

Weber (1904) and Abel (1914) in textbook treatment followed Schlosser and the earlier conclusions of Osborn in believing that a close genetic relationship existed between *Meniscotherium* and the chalicotheres. Weber's classification included Meniscotheriidae in the Condylarthra with full ordinal status for the latter, but Abel (1914) substituted Protungulata for the ordinal name, including it under the superorder Ungulata. This arrangement, of course, prevailed in Abel's revision of Weber's text in 1928.

It appears that neither Matthew nor Gregory followed Osborn in his interpretation of the relationships of *Meniscotherium*. Matthew in 1897 pointed out the various possibilities that had been suggested, and Gregory (1910) noted that, "The manus of *Meniscotherium* has no suggestion of the Chalicother type, . . ." and (1920) that *Meniscotherium* was obviously "not ancestral to the titanotheres, and probably not to the chalicotheres." Matthew made no particular investigation of meniscotheres but in 1899 was concerned that the foot material of *Meniscotherium*, probably that in the Cope collection, did not agree with illustrations by Marsh for "*Hyracops*." However, Granger in his taxonomic revision of the species of *Meniscotherium* in 1915 pointed out errors in reconstruction of the "*Hyracops*" carpus, concluding that there was no reason for distinguishing "*Hyracops*" from *Meniscotherium*.

Ameghino (1893) was particularly critical of the concept that



*Meniscotherium* was ancestral to the chalicotheres. In Ameghino's arrangement the Homalodontotheriidae occupied this position with respect to the chalicotheres of the boreal hemisphere, and the meniscotheres were described as allied with the Proterotheriidae with which they must have had a common but as yet undiscovered ancestry. This was later than Cope's (1891) observation that the dentition of the Macraucheniidae could have been derived from that of the Meniscotheriidae, as well as that the dentition of the Proterotheriidae could easily be derived from that of the Peripitychidae. In 1901 Ameghino went so far as to include within the family Meniscotheriidae various genera of litopterns now divided between the Proterotheriidae and Macraucheniidae. In the meantime, Wortman (1896) attributed the appearance of the Proterotheriidae to a southward migration of the meniscotheres and later (1904) enlarged upon this hypothesis to postulate that not only were the Litopterna direct derivatives of *Meniscotherium* but that all South American ungulates were but modified descendents of North American condylarths.

Cope's suggestion of a condylarthran relationship to the hyracoids, which seems first mentioned in 1882(b) and later reflected in his taxonomic arrangement (1884b), was early championed by Wortman (1886). While Cope was concerned with certain resemblances in the structure of feet, Wortman, in reviewing teeth of *Meniscotherium*, saw a marked indication there of hyracoid affinity and was disposed to regard this genus as the direct ancestor of the Hyracoidea.

Marsh (1892) noted the *Hyrax*-like appearance of the carpals and tarsals which he indicated in his name *Hyracops* but evidently did not regard the relationship as close, as he proposed for the meniscotheres the new ordinal name Mesodactyla and about which he stated as follows: "The teeth are somewhat similar to those of Ungulates, but the rest of the skeleton, especially the limbs and feet, are of a generalized type quite distinct from any hoofed animals known, recent or extinct. Some parts of the structure seem to indicate an affinity with *Hyrax*, but the limbs and feet show characters resembling those of Primates, especially the extinct forms, and likewise seen in Insectivores, and even in some of the Rodents."

A little later that year (1892) Scott, although not certain that *Meniscotherium* was a direct ancestor of the modern hyracoids, was convinced from Marsh's (1892) portrayal of the feet of "*Hyracops*" and from his own study of meniscotheriid premolars that the family should be removed from the Condylarthra and included in the Hyracoidea. In 1913 Scott regarded this arrangement as improbable,

but in the second edition of his textbook (1937) this latter opinion was modified by the statement that the hyracoids were probably derived from Old World condylarths. Schlosser in his study of the Fayum hyracoids (1911) pointed out that although there was a resemblance in foot structure between *Meniscotherium* and the hyracoids, the tooth structure resemblance is with the recent hyracoids and only one Fayum form (*Sagatherium*). Greater divergence was noted with respect to the bunodont hyracoids of the Fayum. Much more recently Simpson (1937) has referred to meniscotheres as "hyracoidlike" and (1945) in commenting on the hyracoids has observed that ". . . no one has ever fully examined and logically interpreted numerous resemblances, probably but not surely superficial, to various other groups, notably to the meniscotheres and notoungulates."

The European Paleocene genera *Pleuraspidotherium* and *Orthaspidotherium* had a varied history of interpreted relationship, as outlined by Teilhard de Chardin (1922), but in their later treatment, following Zittel (1893), came to be regarded by Weber (1904) and Schlosser (in Zittel and Schlosser, 1923), for example, as having condylarth affinities. It may be noted, however, that following his description of these genera in 1878, Lemoine, in 1892 (see Teilhard de Chardin, 1921-1922, p. 37), thought that *Orthaspidotherium* belonged in a position ancestral to the artiodactyls, an idea that was adopted by Schlosser in 1911 (in Zittel and Schlosser). Teilhard de Chardin in 1920 (and 1922) convinced of a closer relationship to the meniscotheres, included both *Pleuraspidotherium* and *Orthaspidotherium* in the Meniscotheriidae. This assignment was adopted by Simpson (1937) but with subfamily separation of *Pleuraspidotheriinae* and *Meniscotheriinae*. In 1929, however, Simpson noted the distinctive features of *Orthaspidotherium* but regarded Schlosser's (Lemoine's 1892) suggestion of an artiodactyl relationship as highly improbable. Most recently D. E. Russell (1964) has described more fully the *Pleuraspidotherium* materials from Cernay and, with detailed consideration of relationships, has followed Teilhard de Chardin and Simpson in including *Orthaspidotherium* as well as *Pleuraspidotherium* in the Meniscotheriidae.

#### GEOGRAPHIC AND GEOLOGIC OCCURRENCE

The known distribution of *Meniscotherium* is included geographically within the states of Wyoming, Colorado, and New Mexico in this country and in Alberta, Canada. Geologically it ranges from

Clarkforkian or latest Paleocene through or nearly through Wasatchian or early Eocene time. As noted by Van Houten (1945) only two Paleocene occurrences are known: a single specimen, the type of *Meniscotherium priscum* Granger (now lost), came from the Clark Fork beds in the Clark Fork Basin; and two lower premolars, one of which ( $Dp_4$ ) was made the type of *Meniscotherium semicingulatum* Russell, came from beds of about this age near Cochrane in Alberta, Canada. The small species of *Meniscotherium* represented in the early Wasatchian at the Bitter Creek and Red Desert localities in southwestern Wyoming, earlier (Gazin, 1962) compared with *M. priscum*, I now find cannot logically be distinguished from *M. tapiacitis*.

Although Granger (1915) has listed *M. tapiacitis* as belonging in the Largo fauna of New Mexico, the single specimen of this very small form may have come from much lower beds, recalling Cope's statement that it was collected "from beds of probably lowest Wasatch age. . . ." The locality is given by Granger as "Alto la Zerta," but I have been unable to find this on any map. Possibly his conclusion that Cope's statement was in error was based on the distribution of *M. chamense*.

With the possible exception of *M. tapiacitis*, *Meniscotherium*, as noted by Granger (1915), Van Houten (1945) and Simpson (1948), is essentially missing from the Almagre facies, but is abundantly represented by *M. chamense* in the Largo facies of the San José sequence in New Mexico. Again in the Wind River Basin, as *M. chamense*, it is known, though sparsely, only in the latest, or in this case, the Lost Cabin fauna. I agree, however, with Van Houten and Simpson that because of the vagaries in distribution this does not warrant a correlation in time between Largo and Lost Cabin as Granger (1915) supposed.

There is no record of *Meniscotherium* in any of the early Eocene or Wasatchian horizons of the Big Horn Basin, following its occurrence in the latest Paleocene Clark Fork beds of the area. On the other hand it is apparently found at all levels in the Wasatchian beds of the southwestern part of the State, except in the southern part of the Fossil Basin and the eastern part of the Washakie Basin. Small *M. tapiacitis* is found in the lower levels of the Knight on both sides of the Rock Springs uplift and has been reported well up in the section, possibly as late as Lysitean, on the east side of the uplift, in the western part of the Washakie Basin near Bitter Creek. *M. cf. robustum* is recorded from an intermediate horizon of the Knight



at Tipton Butte, and an undetermined species is reported (Henry W. Roehler, personal communication) from a semifluvial facies of the Tipton tongue on nearby Table Mountain. Thorpe's species is especially characteristic of the La Barge fauna, but a smaller form which may well be *M. chamense* is abundant in the New Fork in the northern part of the Green River Basin, both faunas being included in Lostcabinian time. Farther east, however, although in the same general basin of deposition for the Wasatch formation, no material of *Meniscotherium* has been reported for the Four Mile, Dad, and typical Cathedral Bluffs faunas. In the Fossil Basin sparse remains have been found on Fossil Butte and in the Gray Bull equivalent west of Elk Mountain, but not in type Knight near Evanston, nor in the Gray Bull equivalent (type Almy) in Red Canyon.

The undescribed collections from the valley of the Colorado River, within the structural basin of Tertiary sediments often referred to as the Piceance Creek Basin in western Colorado, are reported by Van Houten (1945) to include *Meniscotherium* abundantly in the lower fossiliferous level of about mid-Wasatchian age and sparingly in the late Wasatchian upper level. Examination of the materials in the Chicago Natural History Museum, however, has revealed that the information furnished Van Houten for the presence of *Meniscotherium* in the late Wasatchian level was based on a jaw fragment with a single premolar belonging to *Lambdaotherium* rather than *Meniscotherium*. In the list of materials in the Carnegie Museum from the Piceance Creek Basin the species of *Meniscotherium* given is *M. tapiacitis*. Two species, however, are represented in both the Carnegie Museum and the Chicago Natural History Museum collections. In the better documented, more recently collected Chicago materials it is clear that the two species, which may well be *M. chamense* and *M. tapiacitis*, do not occur together but in rather widely separated areas. *M. chamense* occurs to the northwest of the Colorado River in the Roan Cliffs area, whereas all the *M. tapiacitus* specimens were found to the southeast of the river in the general area of Mam Creek. Nevertheless, there is no evidence that the horizons represented are significantly different and may well be mid-Wasatchian.

The rather sporadic distribution of *Meniscotherium* outlined here is summarized in the accompanying chart, and explanation of these apparent anomalies is attempted in the following section concerning environment.



	Alberta, Canada	Big Horn Basin, Wyo.	Wind River Basin, Wyo.	Washakie Basin, Wyo.		Green River Basin, Wyo.	Fossil Basin, Wyo.		Piceance Creek Basin, Colo.	San Juan Basin, N.M.
				East side	West side		North part	South part		
Lost Cabin or equivalent		absent	<i>M. chamense</i> sparse	absent (Cathedral Bluff)	absent (Cathedral Bluff)	<i>M. chamense</i> abundant (New Fork)			absent (Upper fossil level)	
				absent (Dad)	<i>M. sp.</i> (Table Mt.)	<i>M. robustum</i> abundant (La Barge)				
Lysite or equivalent		absent	absent		<i>M. cf. robustum</i> (Tipton Butte & Sand Butte)		<i>M. cf. robustum</i> sparse (Fossil Butte)	absent (Knight Sta.)	<i>M. chamense</i> abundant (Roan Cliffs Area) <i>M. tapiacitis</i> abundant (S.E. of Colorado R.)	<i>M. chamense</i> abundant (Largo facies)
					<i>M. tapiacitis</i> (near Bitter Creek)					<i>M. tapiacitis</i> very sparse (Largo auct. Granger) or <i>M. chamense</i> very sparse (Almagre)
Gray Bull or equivalent		absent	absent (Indian Meadow)		<i>M. tapiacitis</i> (Bitter Creek)	<i>M. tapiacitis</i> (SW of Rock Springs)	<i>M. cf. robustum</i> sparse (W. of Elk Mt.)	absent (Red Canyon, Almy)		<i>M. tapiacitis</i> (Lowermost auct. Cope)
Sand Coulee level		absent		absent (Four Mile)		absent (Buckman Hollow)	<i>M. tapiacitis</i> (NW of Fossil Butte)			
Clarkforkian	<i>M. semiclingulatum</i> sparse (Cochrane)									

Chart 1. - Distribution of species of *Meniscotherium* by horizon in various basins, or areas within basins of deposition.

## ENVIRONMENT

There would appear to be but little doubt that the peculiar distribution of *Meniscotherium* during Wasatchian time is largely the result of environmental factors. Where a local population is well represented in a collection, the absence or abundance of remains of an average-size animal such as *Meniscotherium* would not likely be due to collecting chances or methods. In seeking explanation or some understanding of the factors guiding distribution in such cases, three lines of investigation would seem to offer promise of reward. These would involve information to be obtained from the physical characteristics of the containing sediments, from the associated fauna and flora, and from interpretation of the morphological characters of the animal itself. With respect to the first two of these, we are here favored by an animal that although comparatively abundant in some instances is seemingly rather more selective as to habitat than a number of its contemporaries. It is such discrepancies or anomalies of distribution that present opportunities for comparison of characteristics of the two environments with regard to sediments and the associated biota.

Directing attention first to the sediments, Simpson (1948) has commented on this aspect of the problem relative to the distribution of *Meniscotherium* in the San Juan Basin. The abundance of remains in the red beds of the Largo facies and near absence from the relatively more drab-colored Almagre suggested, as an extension of Van Houten's interpretation, adaptation to a more savannalike environment rather than swampy or more aquatic conditions. While the correlation seems evident here in the "different bulk facies," I find it difficult to extend this demonstration, so far as coloration alone is concerned, to conditions in the Green River Basin. I suspect that the larger species of *Meniscotherium* on other evidence may have favored a more savannalike environment, but probably this is not invariably reflected in coloration. In the upper Knight beds between La Barge and Big Piney, Wyo., where *Meniscotherium robustum* is so abundant, it has been quarried repeatedly in both the massive gray and red beds of the variegated sequence. It should be noted, however, that both kinds of beds appear to be fluvialite and there is rather little difference between them, other than coloration. Moreover, *Meniscotherium* cf. *chamense* is abundant in beds of similar composition in the New Fork sequence, but none of these in the fossiliferous area are red, but neither do they appear paludal. On the other hand similar, but deep red, sandy clays in the Dad

area, both above and below the Tipton tongue, as well as the red beds of the Big Horn Basin are barren of *Meniscotherium*.

A more nearly paludal facies is represented near the base of the Wasatch at Bitter Creek, where colorless or drab sandy shales alternate with coal or peaty layers. *Meniscotherium*, though sparse, is represented here by small *M. tapiacitis*, which may have been less adapted to a savanna environment or was possibly less discriminating in this respect than the larger, later species. It seems possible, moreover, that *M. tapiacitis* may be represented nearly 700 feet above the base of the Wasatch not far from Bitter Creek. Roehler (unpublished charts) has designated the beds at this higher level as in general semifluviatile, although at the fossil site they are indicated as shaly.

The reported occurrence of *Meniscotherium* in the Tipton tongue on Table Mountain might appear disconcerting and contrary to the supposition that the later *Meniscotherium* preferred a savanna environment, but I find that the rock involved is a massive sandstone in a more general facies described by Roehler as semifluviatile, which he has shown as interfingering with typical lacustral sediments of the Tipton tongue.

While supposing a savannalike environment for later *M. robustum* and *M. chamense*, close proximity of a large body of water, the earlier stages of Bradley's Gosiute Lake in southwestern Wyoming, in no way inhibited their range as represented in fluviatile facies interfingering with lacustral. Nevertheless, coincident with the widespread extension of the Green River lacustral facies, the Tipton or Fontenelle tongue—Gosiute Lake encroaching on the marginal lowlands—*Meniscotherium robustum* evidently became extinct. Following retreat of this tongue the form was replaced, as represented in the overlying fluviatile sequence, by a somewhat smaller, possibly more widely ranging species believed to be the Largo *M. chamense*.

The disappearance of *M. chamense* at or near the close of Wasatchian time would seem unrelated to features of the complex of Green River lakes in Wyoming, Utah, and Colorado, because of its known more widespread distribution, such as in the Wind River Basin. The advent, however, of the more extensively distributed Laney member would suggest climatic change of a regional nature coincident with the extinction. Moreover, Bridgerian time in this region is characterized by voluminous ash falls, so clearly demonstrated in the fluviatile sequences interfingering with the Laney, which may have been detrimental to *Meniscotherium* either directly or by altering the environment.



The regional environment revealed from detailed study of Green River sediments by Bradley (1929) and of the Green River plants by Brown (1929, 1934) was previously summarized (Gazin, 1953, 1958) as it pertained to studies of tillodonts and primates. While much of this may bear more directly on the middle Eocene, it does of course include later Wasatchian time during which *Meniscotherium* flourished in the Green River Basin. Bradley in studies of the physical characters of the lake in comparison with other large lakes concluded that the climate, interpreted particularly for the Gosiute Lake region, was characterized by cool, moist winters and relatively long, warm summers. The temperature probably fluctuated widely from a mean annual temperature of the order of 65° F. The rainfall is described as varying with the seasons and fluctuating widely from a mean annual figure somewhere between 30 and 43 inches. He also pointed out that the relief, as it pertains to the height of the rim of the Gosiute drainage basin relative to the floor, was probably greater than now, although the floor of the basin was likely less than 1,000 feet above sea level.

From the paleobotanical evidence for the regional environment Brown has described "a broad, low-lying warm inland region, with shallow ponds, lakes, and marshes, fed by slow streams, which meandered through muddy and sandy swamps as they flowed out of the distant cooler foothills and surrounding mountains." In this connection Bradley (1929), in discussing topography of the ancient Green River basin, observed, "most of the streams within the Gosiute hydrographic basin were apparently rather short and flowed directly into the lake, but those in the eastern part were longer and may have had considerable volume." It is possible that these statements are not truly at variance, since both are of such general application. Moreover, Brown has noted for the entire area of Green River deposits, "that local conditions of climate, influenced in part by mountains that flanked the basin in the north, east and west, might vary considerably in such a basin." Nevertheless, it is in the part of the Gosiute Lake basin where the streams were evidently shorter that *Meniscotherium* most recently flourished. As discussed above, it does not seem to have been present in the eastern part of the basin during later Wasatchian time.

In attempting to understand the differences between Wasatchian faunal assemblages including or not including *Meniscotherium*, there is, unfortunately, no adequate paleobotanical evidence that might be correlated, so that information on possible local differences in the



floristic environment or food supply for the herbivores is not at hand. A comparison of the mammalian faunas, however, reveals other and apparently related discrepancies that are surely significant. Certain of the differences, nevertheless, while provoking speculation, cannot be fully credited because of the sparsity of remains upon which presence was established.

Perhaps the most striking feature revealed in the faunal comparisons made is the seeming incompatibility of *Meniscotherium* and *Phenacodus*. This is most noticeable in the difference between the faunas of the Big Horn Basin and those of the Green River basin. Exception to this relates to the smaller form or forms of *Meniscotherium* which, as well as being found in more paludal sediments, is associated, though very sparsely, with *Phenacodus* in both the Clark Fork and Bitter Creek localities. It may be further noted, however, that in the more abundant materials of the Four Mile fauna, which is close in time to Bitter Creek, some diversity of phenacodonts is represented, but no *Meniscotherium*. Unfortunately, the relative stratigraphic position for much of the Cope collection from the San Juan Basin is not known. Nevertheless, it would seem from Granger's and Simpson's collecting that *Phenacodus* is essentially characteristic only of the Almagre, although one of the specimens mentioned (Granger, 1915) came from the Largo or *Meniscotherium* facies. In the Wind River Basin *Phenacodus* but not *Meniscotherium* occurs in the Lysite, whereas in the Lost Cabin beds both are recorded although *Meniscotherium* is very scarce. Moreover, there is no reported information on the relative stratigraphic position of these, so that no certain conclusions can be drawn. In the Piceance Creek Basin, of the approximately 25 Chicago Natural History Museum specimens certainly identified as *Phenacodus*, only 1 was from the Roan Cliffs area yielding *M. chamense*. Except for three from localities not pinpointed, however, the remainder were from the area southeast of the Colorado River, often in association with *M. tapiacitis*. Finally, *Phenacodus* but no *Meniscotherium* is reported (Peter Robinson, MS.) for the Wasatchian of the Huerfano Basin in Colorado.

Among other elements that seem foreign to the *Meniscotherium* environment are *Homogalax* and *Ectocion*, although the evidence here may not be so convincing, inasmuch as these two are rather sparsely represented outside the Big Horn Basin. For example, *Ectocion* is found in the Clarkforkian beds at Buckman Hollow, Four Mile Creek, and Lost Cabin, and *Homogalax* at Bitter Creek,

Four Mile Creek, and Dad. Several specimens of *Homogalax* or a closely related form in the rather scant collections from the Wasatchian beds near Dad, Wyo., are noteworthy because no isctolophid is represented in the contemporary La Barge fauna. *Homogalax* and *Meniscotherium*, small *M. tapiacitis*, have been reported together only at Bitter Creek.

Discrepancies in the distribution of the smaller artiodactyls *Diacodexis* and *Hexacodus* may also merit discussion. *Diacodexis*, while widely distributed, is abundant only in the Big Horn Basin. *Hexacodus*, on the other hand, with the exception of a single Gray Bull specimen, has so far been found only in southwestern Wyoming. Distribution of these may in a general way be related to the environment of *Meniscotherium*, but it must be noted that relatively scant remains of *Diacodexis* have been found in nearly all *Meniscotherium* occurrences. *Diacodexis*, however, is outnumbered by *Hexacodus* better than 5 to 1 in the La Barge fauna.

Of the remaining subungulate and ungulate forms of the Wasatchian, *Hyopsodus* is nearly universal in occurrence. It is possibly of more than casual interest, however, that with the exception of three specimens of *H. walcottianus* reported from the Lost Cabin beds and one from the New Fork, the larger species of *Hyopsodus*, including *H. browni*, *H. powellianus*, and possibly *H. walcottianus*, seem to avoid *Meniscotherium* or vice versa. Equally widespread *Hyracotherium*, however, would appear in no way influenced by the range of *Meniscotherium* or the factors controlling its distribution. The same may be said of *Heptodon* and *Lambdotherium*, although these are known only from later portions of Wasatchian time, and *Heptodon* seems to have a more restricted geographic range, but unrelated to the distribution of *Meniscotherium*.

*Coryphodon* has a distribution which in some ways appears at variance with that of *Meniscotherium*, but having collected the two in close proximity at various localities in the Knight, I suspect that abundance of the former is more closely correlated with time. It seems everywhere well represented in Gray Bull levels of the Willwood, Wasatch, and San José formations and particularly abundant in the lowest levels, to judge by its occurrences in the Washakie and Fossil Basins. It is missing or rare in Lysite levels, except possibly for the Fossil Basin, but then again it is not rare in the later Wasatchian of the Wind River and Green River Basins, in the latter being more closely associated with large *Meniscotherium*.

The scarcity of the herbivores *Esthonyx* and *Ectoganus* or *Sty-*

*linodon* in the basins of southwestern Wyoming and rather better representation in the Big Horn and San Juan Basins may well be related to environmental differences, but these forms are comparatively rare in middle and later Wasatchian levels in any case, so that no significant correlation with *Meniscotherium* one way or the other is evident. It may, however, be of interest to note that of the few San Juan Basin *Esthonyx* specimens for which adequate locality data are known, about a third are from the Largo or *M. chamense* beds, and that Roan Cliffs or *M. chamense* area specimens represent a roughly similar ratio of the Piceance Creek Basin materials. The species of *Esthonyx* are comparable in size to those of *Meniscotherium*, and lower molars show a rather similar selenodonty. The progressive development of the anterior portion of the dentition in both *Esthonyx* and *Ectoganus*, however, suggests food-getting habits rather different from those of *Meniscotherium*.

Among the unguiculate forms, such as the insectivores, primates, rodents, and carnivores, essentially not in competition with *Meniscotherium* as far as food supply is concerned, I have been unable to detect any important discrepancies in distribution that might be correlated. Most such orders include a diversity of genera for Wasatchian time, but only a few of these can be regarded as truly abundant in any instance. Primates, however, because of their special connotation as to environment draw attention. The La Barge fauna, as well as that represented at Bitter Creek, includes a rather striking diversity of primates and certain of these are comparatively well represented. From this we may assume that locally trees were plentiful in the savannalike environment postulated for *M. chamense* and *M. robustum*, as well as in the more paludal environment that we find for *M. tapiacitis*.

The morphological features of *Meniscotherium* which relate most directly to the environment are, of course, the characteristics of the dentition and feet, or adaptation to food and terrain. The anterior part of the dentition is relatively unspecialized, but the cheek teeth, upper and lower, are surprisingly precocious both in degree of selenodonty and in tendency toward molarization of the premolars. Teeth of this kind are better adapted to a more grazing habit, permitting harsher vegetation, than are the more bunodont teeth in other groups, such as contemporary *Hyracotherium*. A rather similar type of tooth structure is seen in the living hyracoids of Africa. Although these latter show a different incisor specialization, molarization of the premolars has proceeded to the anterior extremity of the series.



The hyrax *Procavia* is reported (Coe, 1962) to be selective in its feeding habits with a preference for grasses, mosses, and certain higher plants with succulent leaves. There is no paleobotanical evidence for grasses during the early Eocene, but the grasslike sedges and certain of the possibly harsher elements of the flora may have been more suitable for *Meniscotherium* than for *Phenacodus* or *Hyracotherium*. No doubt mosses and a variety of succulent leaves were available for selection. *Phenacodus*, on the other hand, quite possibly had a more omnivorous habit.

The feet of *Meniscotherium* are moderately robust but show the structural weakness of a serially arranged condylarthran tarsus, somewhat less evident in the carpus. The feet are pentadactyl, but with the lateral digits in the pes, particularly the hallux, reduced. The ungual phalanges are elongate and distally flattened dorsoventrally or spatulate, much more so than in *Tetraclaenodon* but not so broadly as in *Phenacodus*. The structure of the foot is rather similar to that of the hyrax in the serial arrangement of the tarsus, somewhat less so in the carpus, and the feet have about the same relative size although they are a little more robust. They differ most noticeably in the articular arrangement between the tarsus and the tibia and fibula and in less reduction of the lateral digits and ungual phalanges. The lateral digits of the pes are lost in the hyrax, and the pollex (only) is vestigial in the manus. The distal phalanges, moreover, while broadly articulating with the second phalanges, are scarcely more than nubbins of bone in the hyrax.

Although the hyrax has a plantigrade foot with pads developed from the nails to the carpus and tarsus, I suspect that *Meniscotherium* was digitigrade or at least semidigitigrade, to judge by the rather different appearance of the inferior margin of the calcaneum. That in the hyrax is more distinctly flattened. The elongate distal phalanx in *Meniscotherium*, with the dorsoventrally somewhat flattened nail-like hoof interpreted, and the character of the articulation between the various phalanges suggest that all these, at least of the three median digits, rested on the ground. From these considerations it would appear that the weight was borne essentially on the ends of the metapodials, quite unlike the hyrax. Any possible interpretation of habit by analogy of foot structure is further complicated by the fact that remarkably different habits are shown by different groups of procaviids. While *Procavia* and *Heterohyrax* are ground- and rock-dwelling forms, *Dendrohyrax* lives in trees. There seems to



be little or no actual difference in foot structure among these—a versatility attributed to the characteristics of the foot pads.

I see no difficulty in attributing a ground habit in a savannalike environment to *Meniscotherium*, as suggested for the two larger species; nevertheless, the foot structure seems rather primitive so that a variety of conditions might be included. The readily divergent, although somewhat reduced, pollex and hallux; the flexibility of the foot articulations with tendency toward supination of the feet, particularly noted for the manus; and the indication of strong abductors and adductors suggest that adaptability may have extended to climbing. As a herbivore the comparatively weaker foot structure implied in the near serial arrangement, in comparison with contemporary perissodactyls, suggests less potential toward a cursorial habit, Kowalevsky's inadapive type, possibly contributing to extinction.

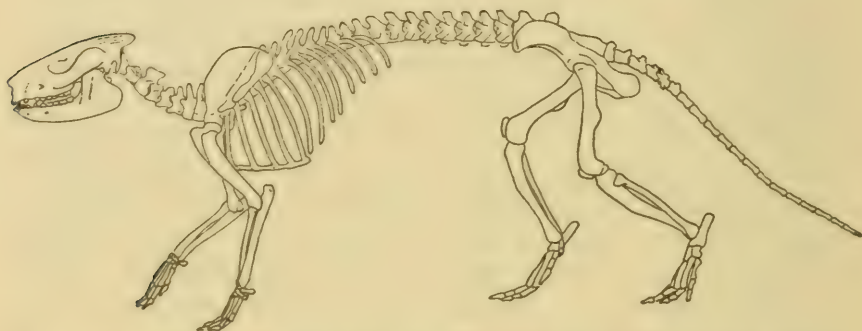


FIG. 1.—*Meniscotherium chamense* Cope. Drawing based on composite skeleton in the American Museum of Natural History. Largo beds of San José formation, San Juan Basin, N. Mex.

Cope (1884b) pointed out that *Meniscotherium* had a relatively larger brain than *Phenacodus* and that the oblique articular surfaces of the cervical vertebrae indicated the elevation at which the head was held. In his "restoration" of *Meniscotherium* he concluded that the body had the robust proportions of a raccoon, with the fore and hind legs rather short and of equal length (see fig. 1).

#### CLASSIFICATION

Condylarthra Cope, 1881

Meniscotheriidae Cope, 1882

*Meniscotherium* Cope, 1874

Synonym.—*Hyracops* Marsh, 1892

Type species.—*Meniscotherium chamense* Cope

*Meniscotherium chamense* Cope, 1874

*Synonyms*.—*Meniscotherium terraerubrae* Cope, 1881; *Hyracops socialis* Marsh, 1892

*Type*.—Right maxilla, U.S.N.M. 1093, with  $M^1$ - $M^3$  and part of  $P^4$ .

*Horizon and locality*.—San José formation, San Juan Basin, N. Mex.

*Range*.—Largo facies, San Juan Basin, N. Mex.; mid-Wasatchian, Piceance Creek Basin, Colo.; Lost Cabin, Wind River Basin, Wyo.; and New Fork, Green River Basin, Wyo. Middle and late Wasatchian early Eocene.

*Meniscotherium tapiacitis* Cope, 1882

*Type*.—Portions of both rami of mandible, A.M. 4425, with  $P_3$ - $M_3$  represented.

*Horizon and locality*.—San José formation, San Juan Basin, N. Mex.

*Range*.—San Juan Basin, N. Mex.; mid-Wasatchian, Piceance Creek Basin, Colo.; early to mid-Wasatchian, Green River Basin, Wyo.

*Meniscotherium priscum* Granger, 1915

*Type*.—Portion of left ramus of mandible, A.M. 16145, with  $Dp_4$  and  $M_1$ .

*Horizon and locality*.—Clarkforkian late Paleocene, Clark Fork Basin, Wyo.

*Range*.—Not known outside occurrence of type.

*Meniscotherium semicingulatum* Russell, 1929

*Type*.—Right  $Dp^4$ , Univ. Alberta, Dept. Geol. 120.

*Horizon and locality*.—Late Paleocene (?), Cochrane, Alberta, Canada.

*Range*.—Not known outside occurrence of type.

*Meniscotherium robustum* Thorpe, 1934

*Type*.—Skull and lower jaw, Y.P.M. 10101.

*Horizon and locality*.—Knight beds near Aspen, Wyo.

*Range*.—Middle to late Wasatchian Knight beds beneath

Fontenelle or Tipton tongue of Green River formation in southwestern Wyoming.

Among the foregoing I suspect that only three species are valid. These I regard as *M. chamense*, *M. tapiacitis*, and *M. robustum*. Although there would appear to be certain characters other than size of the skull and postcranial skeleton that may be significant in distinguishing between the two larger forms *M. robustum* and *M. chamense*, size seems to be the only generally definable feature in their separation and is consistently applicable in the Wyoming area. The much smaller *M. tapiacitis* type has been characterized by the weakness of the metastylids of the lower molars, but I find this is somewhat variable in other materials, so that its better development in the correspondingly small *M. priscum* type is probably unimportant. The latter is tentatively retained only because of its earlier geologic age. *M. semicingulatum* also may not be definable, since its description is evidently based essentially on a deciduous lower premolar. Its size would not distinguish it from *M. chamense*, but its geographic

separation, as well as its possible age difference, may justify tentative recognition.

While the moderately conservative range in size of *M. robustum* in Knight beds beneath the Fontenelle tongue of the Green River in southwestern Wyoming is clearly separable from that of the smaller, typical *M. chamense* size from above the Fontenelle tongue, the somewhat earlier situation in the San Juan Basin is not so clearly resolved. The range in size there is much greater and is said to be continuous so that no logical separation could be made between *M. chamense* proper and *M. terraerubrae*. Granger (1915) illustrated this by regarding *M. terraerubrae* as a subspecies of *M. chamense*, but this is not strictly tenable unless some ecologic barrier or stratigraphic difference can be shown. With the range in size evident I suspect that there is more than one species represented, not clearly definable in the material represented, or there is a strong potentiality for such a split.

There is no evidence of a developmental sequence from *M. tapia-citis* through *M. chamense* to *M. robustum* as might be suggested by size, because in about mid-Wasatchian time approximately contemporary occurrences are known, although the species are not actually found associated. This is further emphasized by the survival of *M. chamense* into later Wasatchian time than *M. robustum*.

#### THE SKELETON OF MENISCOTHERIUM, WITH NOTES ON PHENACODUS, HYOPSODUS, AND OTHER CONDYLARTHS

##### SKULL

In overall appearance the skull of *Meniscotherium* is relatively broad across the frontals, and the robust rostrum is approximately equal in length to the more slender cranial portion. The posterior extremity of the tooth row and the orbital constriction across the frontals come very near a mid cross section of the skull. In longitudinal profile the dorsal surface is only gently convex to nearly straight. The basilar axes, palatal and basicranial, appear nearly parallel but intersect at a relatively low angle in the least distorted specimens. Notable are the prominence of the postorbital processes of the frontals, the extent to which the squamosal portion of the zygomae flare upward and inward, the backward deflection of the lambdoidal crest and the marked length of the paroccipital processes. Moreover, the cheek teeth are strikingly selenodont, and accompanying this the glenoid surface for articulation of the lower jaw is biconcave and anteroposteriorly elongate.



*Dorsal view.*—In dorsal view (see pls. 1 and 2) the rostrum does not taper forward nearly so abruptly as shown by Cope (1884b, pl. 25f, fig. 13a). The nasals are broad and elongate, extending from about even or slightly forward of the greatest anterior extremity of the premaxillae to a posterior limit well into the frontal segment, nearly halfway in some specimens. They are wide anteriorly, at the anterior extremity of the naso-premaxillary suture, and somewhat constricted about midway in their length, near the premaxillo-maxillary suture, but reach the greatest width where the frontals join the maxillae. Posterior to this they taper gradually, and about a third of the way across the frontals they are abruptly rounded off with a strong reentrant of the frontals along the midline of the skull. The nasals are very much like those in *Phenacodus* except that in the latter there is greater penetration into the frontal area and the greatest width is carried posterior to the fronto-maxillary suture well into the frontal area. In marked contrast the nasals in *Hyopsodus* terminate rather abruptly posterior to the fronto-maxillary suture.

The frontals are broad and flat between the orbits and reach forward to contact with the maxillae, although a short distance laterally the frontals and maxillae are widely separated by the lachrymals. Posteriorly the frontals generally show a shallow depression between the postorbital processes which is posteriorly defined by the strong temporal ridges. The latter converge abruptly medial and posterior to the postorbital processes.

The frontals in *Phenacodus* are much more convex transversely, and a longitudinal convexity is better emphasized somewhat farther forward over the posterior region of the nasals. The postorbital processes are not nearly so well defined in *Phenacodus*, and the temporal crests converge posteriorly much more gradually than in *Meniscotherium*. The frontals in *Hyopsodus* are gently convex transversely, and there are no postorbital processes. The comparatively weak temporal crests diverge forward with little or no flexure to become the orbital rims.

From the union of the temporal crests at about the postorbital constriction in *Meniscotherium* the well-developed sagittal crest extends nearly straight over the elongate-appearing cranial portion to divide again into the two posteriorward flaring halves of the lambdoidal crest. The most conspicuous feature of the elongate temporal fossae is the nearly a dozen or more prominent vascular foramina in the posterior portion of the areas, for the most part near the parieto-squamosal suture but lacking any symmetry with respect to



the median plane of the skull. The area of each fossa is divided about equally between the parietal and squamosal, although the lambdoidal crests are for the most part formed of a fringe of the exoccipitals. There is no evidence of an interparietal. In *Phenacodus* the cranial portion appears relatively shorter than in *Meniscotherium*. This is effected in part by the more gradual convergence of the temporal crests resulting in a somewhat more posterior position of the postorbital constriction. It may be further noted that the lambdoidal crests do not project out over the occiput so markedly and are relatively broader in *Phenacodus*. *Hyopsodus* on the other hand exhibits a rather elongate cranial portion, and the occipital crest turns sharply upward, producing a more distinct dorsal concavity in the posterior portion of each of the temporal fossae. An irregular cluster of vascular foramina is noted near the parieto-squamosal suture in the lateral portion of these depressions.

*Lateral view.*—In lateral view (see pls. 1-3) the premaxilla of *Meniscotherium* is seen as a narrow bar or plate extending from the incisors upward and backward along the anterior margin of the maxilla and wedging out posteriorly between the maxilla and nasal. Only a short length of nasal extends free anterior to the premaxilla. In uncrushed skulls the maxilla is moderately deep and exhibits a large infraorbital foramen approximately above the contact between the third and fourth premolars, well above the tooth row and well forward of the orbital margin. The lachrymal bone extends forward a short distance anterior to the orbital rim and upward almost but not quite to the nasals. In its juncture with the jugal below it excludes the maxilla from the orbital rim. The lachrymal foramen has a position essentially on the orbital rim to just within the orbital fossa, where it may be partially concealed by the lachrymal tubercle on the rim. The anterior margin of the orbit is above approximately the anterior margin of the second molar, not so far forward as in *Ectocion* or the later hyracotheres, and the lower margin is not deflected outward on the jugal so noticeably as in those forms. The jugal is moderately deep and forms a strong, dorsoventrally deep attachment to the maxilla, but the crest of the zygoma does not carry so far forward on the face. Posteriorly the zygomatic process of the squamosal is strikingly deep above the glenoid surface, and the upper portion of the flare is turned decidedly inward toward the crest of the ascending ramus of the mandible and the sagittal crest of the skull. Posterior to the postglenoid process the crest of the zygoma extends onto the cranium defining the lower margin of

the temporal fossa, and terminates in the lambdoidal crest just above the mastoid portion.

The *Phenacodus* skull in lateral view shows a relatively greater depth of the snout and a more distinctly convex longitudinal profile. The premaxilla is more slender, and the portion carrying the incisors projects forward, more shelflike than in *Meniscotherium*. The anterior portion of the zygoma joins the rostrum much as in *Meniscotherium*, but the orbit is slightly more posterior with its anterior margin approximately above the middle of the second molar and the larger infraorbital foramen opens anteriorly a little farther back, more nearly above the first molar. The lachrymal foramen is similarly placed just within the orbital rim partially concealed by the somewhat larger lachrymal tubercle. As well as being more subdued, the postorbital processes are more posteriorly placed with respect to the tooth row, and as previously noted the postorbital constriction is distinctly farther back. It is particularly noticeable that the zygomatic process of the squamosal in *Phenacodus* is relatively shorter and much more slender than in *Meniscotherium*, lacking the dorsal flare above and anterior to the region of the glenoid surface. In small *Hyopsodus* the orbit is located with respect to the dentition about as in *Meniscotherium*, but the infraorbital foramen is a little farther forward and perhaps relatively closer to the tooth row. Moreover, the jugal seems relatively deep for so small a form.

Within the orbital fossa of *Meniscotherium* the orbital plate of the maxilla presents a relatively large, broadly concave superior surface exhibiting the large posterior opening of the infraorbital canal at its anterior extremity. The sphenopalatine foramen opens near its posterior margin but faces laterally in the adjacent ascending plate of the palatine, very near the notch in the posterior margin of the horizontal plate of the palatine. Immediately below but actually confluent with the larger aperture of the sphenopalatine foramen is the more dorsally facing posterior opening of the posterior palatine foramen. Farther back in the fossa the optic foramen, if correctly identified, is located slightly higher and well in advance of the sphenoidal fissure, apparently near the anterior margin of the orbitosphenoid. Posterolateral to the sphenoidal fissure and lower but not far removed is the anterior opening of the alisphenoid canal which, as determined from damaged specimens, is confluent in its anterior portion with the foramen rotundum.

The orbital plate of the maxilla in *Phenacodus* is more elongate and relatively narrower than in *Meniscotherium*. The posterior pala-

tine foramen is nearly confluent with the sphenopalatine foramen somewhat as in *Meniscotherium*, and both are above and a little forward of the notch in the posterior margin of the palatine between the maxillary tuberosity and the ascending plate of the palatines. In *Phenacodus*, however, these foramina are posterior to  $M^3$ , whereas in *Meniscotherium* they are anterior to the posterior margin of the tooth series.

The optic foramen is relatively closer to the sphenoidal fissure in *Phenacodus*, the actual distance being approximately the same as or somewhat less than in much smaller skulls of *Meniscotherium* and *Ectocion*. Also, the anterior opening of the alisphenoid canal seems more closely appressed and immediately lateral to and somewhat lower than the sphenoidal fissure in *Phenacodus*. In the material observed I have been unable to determine whether there is a foramen rotundum confluent with the anterior opening or whether the second branch of the trigeminal nerve passed through the sphenoidal fissure with the first as Simpson (1933) has suggested. I suspect that these nerves emerged separately as seems demonstrated in *Meniscotherium*, although they possibly left the cranial cavity together through a posterior confluence of the foramen rotundum and sphenoidal fissure. The Cope endocast of *Phenacodus* is ambiguous in this respect, as the two sides are not alike in this area.

In *Hyopsodus* the orbital plate of the maxilla appears relatively short and wide with the long diameter nearly transverse, and the sphenopalatine foramen is about even with or slightly posterior to the hind margin of the last molar. The optic foramen is well in advance of and a little higher than the sphenoidal fissure. As observed in *Phenacodus*, it is just ahead of the anterior extremity or angle of the crest which forms the inferior border of the temporal fossa—the forward extension on the cranium of the anterior root or crest of the zygomatic process of the squamosal. In *Meniscotherium* this crest is not so well defined and does not coincide with the ledge or bulge immediately above the sphenoidal fissure which it forms in *Phenacodus* and *Hyopsodus*. The alisphenoid canal, if correctly interpreted for *Hyopsodus*, is decidedly elongate and the anterior opening, presumed confluent with the foramen rotundum, is somewhat less distinctly lateral to the sphenoidal fissure. It appears as a marked elongation or extension posteroventrally of the opening of the sphenoidal fissure.

*Occipital view.*—In an occipital view the most striking feature of *Meniscotherium* is the overhang of the occipital crest which con-



sists of two fanlike projections of the supraoccipital supported in the more mature specimens by two low and broadly rounded ridges diverging upward from the broadly convex posterior surface of the occiput above the foramen magnum. Such development of the lambdoidal crest tends to expand posteriorward the area of origin for the temporal muscle and presents a strong rim of attachment for the trapezius, splenius capitis, etc., which function in raising the head. The lateral margins of these two fanlike projections extend downward and forward, becoming nearly parallel, to a point near the upper extremities of the mastoid portions. Below this a lateral flare of the lambdoidal crest on each side is developed on the squamosal. The mastoid portion of the periotic is exposed in a depressed area on either side in the lower half of the occiput, near the lateral margin. It is most broadly exposed in the upper portion and nearly pinches out below between the very elongate paroccipital process and the weakly developed mastoid process of the squamosal. Possibly the sterno-mastoid muscle was attached to the crest of the squamosal which extends as a prominent protecting rim to the lateral margin of the mastoid.

The occipital view of the *Phenacodus* skull is rather similar, although the two flaring projections of the supraoccipital are relatively broader and less overhanging, and the widely diverging ridges on the occipital surface, serving as buttresses to the lambdoidal flares, are more strongly rounded and extend upward and outward from about the foramen magnum. Between these buttresses the occipital surface is triangular and gently concave, lateral to them the surface on each side, including the exposed portion of the mastoid, faces more laterally than in *Meniscotherium*. Moreover, the mastoid portion does not become so nearly pinched out ventrally.

In *Hyopsodus* the flaring of the occipital crest is directed more dorsally and the buttresslike ridges seem comparatively weak and widely separated and may not be well defined. The mastoid portions of the occipital surface, as in *Phenacodus*, face more laterally, and in marked contrast to *Meniscotherium* increase in breadth of exposure ventrally.

*Palatal view.*—In a ventral view the palate of *Meniscotherium* (see pls. 1 and 2) is seen to be moderately broad and elongate with the lingual margins of the cheek teeth aligned nearly parallel on the two sides, although the palate may be slightly constricted between first premolars. Anteriorly it is about evenly rounded within the margin of canines and incisors. The anterior palatine foramina seem



comparatively small but in no specimen are they clearly defined, and the extent of premaxillary exposure in the palatal view would appear to be limited to the rim of bone supporting the incisors anterior to the canines. In the posterior portion of the palate the palatines extend forward to a position about even with the anterior portion or margin of the first molar. The posterior palatine foramina may show one or two openings on each side, on or near the suture between the maxillae and palatines, inward from about the posterior portion of  $M^1$ . Posteriorly this suture comes near or reaches the alveolar margin of the last two molars. The posterior narial aperture is a little more than half the width of the palate between the third molars and extends forward to a position about even with or slightly in advance of the anterior margin of the third molars. The forward margin of the aperture is gently rounded to nearly rectangular in outline and exhibits a slightly everted liplike rim in a forward continuation of the inferior margin of the ascending plates of the palatines bounding the narial aperture. Lateral to this lip or crest and medial to the prominent maxillary tuberosity, the posterior margin of the palatines may show a pronounced though broadly rounded notch.

The palate in *Phenacodus* is lower with respect to the basicranium than in *Meniscotherium*, in keeping with the relatively deeper rostrum of *Phenacodus*. It is also noted that the notch between the ascending plate of the palatines and the maxillary tuberosity is more constricted in *Phenacodus* and extends forward more deeply grooved on the ventral surface of the palate.

The palate in *Hyopsodus* is rather like that in *Meniscotherium* and *Phenacodus* with the palatines extending forward to about even with the anterior margin of the first molars. Also, the anterior margin of the posterior narial aperture shows the inflected liplike rim or crest seen in both *Meniscotherium* and *Phenacodus*, but this margin does not extend so far forward in the palate as in *Meniscotherium*. Its anterior margin seems about even with the posterior portion or margin of the last molar. Moreover, the maxillary tuberosity is much nearer the lateral margin of the narial aperture so that there is only a very small notch between them in contrast with the deep and broadly open saddle in *Meniscotherium*.

*Basicranium*.—The basicranium in *Meniscotherium* (see pl. 3) appears relatively elongate. This is noticeable in the length of the mesopterygoid fossa and in the posterior position of the occipital condyles with respect to the glenoid surfaces for the mandible. The lateral walls of the mesopterygoid fossa extend posteriorly to dis-

appear at a point just median to the foramen ovale. The anterior portion of each wall is composed rather largely of the vertical or ascending plate of the palatines, and a well-developed and widely open pterygoid fossa extends anteriorly well into and dividing the lower margin of these plates posteriorly. The pterygoid plate of the alisphenoid, the principal element composing the outer wall of the pterygoid fossa, is thicker and more sturdy than the pterygoid proper forming the medial wall, and its ventrolaterally directed lower margin exhibits a hamularlike process, possibly better developed than the hamular process of the pterygoid, although this is uncertain because in no specimen at hand does the lower margin of the pterygoid appear to be complete or undamaged. Immediately posterior to the pterygoid fossa, just above the point where the pterygoid and pterygoid plate of the alisphenoid join, is the posterior opening of the alisphenoid canal, lower and rather well in advance of the foramen ovale. The alisphenoid canal is essentially within the lateral wall of the mesopterygoid fossa opening at a distinctly ventral position on its posterior margin. From its posterior extremity the course of the canal, distinctly upward and forward to its junction with the foramen rotundum, has been observed in damaged specimens. Posterior to this junction a fair-size opening on the dorsomedial wall of the canal, about midway in its length, has been observed in one specimen, but the course of this foramen has not been determined. In all probability it enters the body of the basisphenoid.

The foramen ovale, well removed from the alisphenoid canal in *Meniscotherium*, is lateral to and may be slightly in advance of the anterior margin of the foramen lacerum medium. Extending posteriorward into the otic fossa from the medial margin of the foramen ovale is a very feeble crest which would seem to define the path of the eustachian tube. From the posterior margin of the foramen ovale, however, there is a very prominent and anteroposteriorly elongate process or crest, the styloid process of Cope, medial to and well separated from the postglenoid process, which apparently consists of laminae of both the alisphenoid and squamosal. Its position is near or about that of the angular spine of the alisphenoid in man which supports a portion of musculature of the soft palate and of the tympanum. Nevertheless, I suspect that here it is homologous to the prominence in this position in certain other mammals, such as the oreodonts, where it forms a pedicle for support of the anterior portion of the bulla. No tympanic bulla has been discovered during preparation of any of the *Meniscotherium* cranial portions. It may

not, however, have been fully ossified or possibly was loosely attached and invariably lost.

The glenoid surface for articulation with the lower jaw is broadly concave transversely as well as fore and aft, with its longest diameter extending anteroexternally. While this would appear to be nearly a ball-and-socket arrangement, considerable forward motion of the jaw is permitted. There is a prominent but relatively narrow postglenoid process, and posteromedial to it is a comparatively large postglenoid foramen. It is interesting to note that in one specimen (see pl. 1) the opening of the postglenoid foramen on the left is through the squamosal but on the right its aperture is bounded medially by a portion of the petrotic. Posterior to the postglenoid process the squamosal is broadly concave for the audital tube. This space is bounded posteriorly by a rather weak mastoid process which is nearly pinched out between the descending plate of the squamosal and the very elongate paroccipital process. The striking development of the paroccipital process is indicative of the significance of the digastric muscle which would extend forward to the inner part of the anterior portion of the lower margin of the jaw, possibly also development of an occipito-mandibularis to the posterior margin of the jaw as described by Sisson for the horse, which shows comparable development of this process.

The hypoglossal or condylar foramen is large and circular in outline and lies about in the middle of a depression between the paroccipital process and the occipital condyle on each side. The foramen lacerum posterius is a more elongate, slitlike and medially constricted aperture lying at the anteromedial root of the paroccipital process and bounded forward by the petrosal. I suspect that the constriction of this slit tends to define the jugular (more lateral) portion as partially distinct from the somewhat wider part for nerves IX, X, and XI.

Although much of the *Phenacodus* skull material is rather poorly preserved or not completely prepared in the basicranial area, there would appear to be a number of differences from *Meniscotherium* worthy of comment. There is less evidence for a so well developed pterygoid fossa in *Phenacodus*, suggesting less significance for the internal pterygoid muscle. Its development in *Meniscotherium* would probably correlate with the relatively deeper and more extended angle of the lower jaw. The foramen ovale occurs just lateral to the posterior extremity of the pterygoid flange but is relatively farther forward, much closer to the alisphenoid canal and farther removed from



the auditory chamber than in *Meniscotherium*. Moreover, the foramen ovale is not followed by a so well defined crest. The basi-sphenoid and basioccipital are relatively broad and the ventral surface appears somewhat more convex longitudinally. This may in part be effected by the more prominent development of the area of muscle attachment that would suggest better development of the rectus capitis anterior major that functions in depressing the snout. The glenoid surface for articulation of the lower jaw is not nearly so concave and with less evidence of the fore and aft motion of the jaw interpreted for *Meniscotherium*. The space between the postglenoid process and the mastoid process, which would be occupied by the audital tube, seems relatively shorter anteroposteriorly. The mastoid exposure, however, between the weak mastoid process of the squamosal and paroccipital process is much broader than in *Meniscotherium*. The paroccipital process of *Phenacodus*, as noted, is much less developed. The hypoglossal or condylar foramen is farther forward in *Phenacodus*, as is also the auditory chamber with the petrosal.

The relatively elongate basicranium of *Hyopsodus* resembles that of *Meniscotherium* in a general way, although there are noticeable differences in detail. In the skull material available it would appear that the pterygoid fossa was significantly developed, and as in *Meniscotherium* there is evidence that the lateral wall or descending pterygoid plate of the alisphenoid was stronger and better developed than the pterygoid proper which defined the medial wall of the fossa. The posterior margin of the pterygoid plate of the alisphenoid ascends steeply to a point near or immediately in front of a somewhat elongate aperture which may well be the confluence of the foramen ovale and the posterior opening of an alisphenoid canal, if the latter is present. This is decidedly different from that found in *Meniscotherium* where the foramen ovale and alisphenoid canal are widely separated. As in *Meniscotherium* there is a strong crest posterolateral to the foramen ovale made up of plates from the alisphenoid and squamosal, but more distinctly lateral in *Hyopsodus* and with less participation of the alisphenoid. This leaves a much wider separation between the crest and the foramen lacerum medium. A broad groove in the alisphenoid for the eustachian foramen is relatively closer to the foramen lacerum medium and better separated from the crest or pedicle, attributed to a possible bulla, than in *Meniscotherium*. There seems rather less of the mastoid exposed posterointernal to this crest and lateral to the tegmen tympani, suggested as a position of attachment for the annulus in *Meniscotherium*. External to this crest and decid-



edly closer is the glenoid surface for the lower jaw articulation. This articular surface though slightly concave transversely is not nearly so much so as in *Meniscotherium*, and its long axis is not nearly so oblique. There is a well-developed postglenoid process posteromedial to the center of the glenoid surface, and immediately posterointernal to the process is a large postglenoid foramen with its aperture entirely surrounded by the squamosal. The broad arch of the squamosal over the external auditory meatus extends posteriorly down the anterior surface of the moderately developed mastoid process, and the relatively greater ventral exposure of the mastoid bone than in *Meniscotherium* causes the position of the audital tube to be relatively farther forward from the condyles and more widely separated from the paroccipital process. The paroccipital process is not complete in any specimen at hand, but its root suggests that it was fairly long and slender, although probably not so elongate as in *Meniscotherium*. The condylar or hypoglossal foramen is located decidedly medial and somewhat posterior to the paroccipital process, close to and partially concealed by the posteroventral margin of the condyle.

*Periotic.*—Ventrally the petrosal of *Meniscotherium* presents an almondlike oval to nearly triangular shape with its broad surface facing anterolaterally and ventrally, and its long axis extending anteromedially. Posterior to the promontorium the transversely elongate fenestra rotunda faces downward and outward as well as slightly backward, and anterodorsal to it the smaller fenestra ovalis faces almost directly outward. On the ventrolateral surface of the petrosal there can be distinguished a sinuous trace or broad groove from the medial margin of the fenestra rotunda, adjacent to the foramen lacerum posterius forward around the medial portion of the promontorium, then anteromedially to the apex of the petrosal. There would appear to be a branch extending over the anterior portion of the promontorium to the fenestra ovalis. One is tempted to interpret this as the position of the internal carotid and its stapedia branch; however, I am inclined to consider the course of the internal carotid as more medial with respect to the petrosal, as there is a broad groove in the basioccipital that faces ventrally in its hinder part, medially adjacent to the posteromedial angle of the petrosal, where the latter solidly abuts the basioccipital. Forward, this groove turns outward along the lateral margin of the basioccipital and adjacent to the ventromedial margin of the petrosal to near the anterior extent of the basioccipital and the apex of the petrosal where the groove opens

broadly into the foramen lacerum medium, and where the internal carotid would enter the cranial cavity. This groove is probably not the inferior petrosal sinus for a vein, as posteriorly it does not seem to join or even approach, as far as visible, the jugular or foramen lacerum posterius. I suspect the above-mentioned grooves on the ventrolateral surface of the petrosal may be for branches of a tympanic nerve plexus.

In the absence(?) of an ossified bulla it may be further observed and interpreted that the facial nerve emerged from the petriotic at an aperture in the roof of the tympanic chamber anterodorsal to the fenestra ovalis, extending downward, then flexing backward lateral to the fenestra ovalis into the sulcus facialis which also housed the stapedial muscle dorsoexternal to the fenestra rotunda. At this point the facial nerve was again directed downward and slightly backward at the anterointernal root of the small mastoid process. Medial to this point of departure there is a small pedicle, evidently the tympanohyal, on a posteriorly directed crest or ridge at its union with the posterior rim of the fenestra rotunda. This ridge separates the above fossa for the facial nerve from the foramen lacerum posterius and joins the petrous and mastoid portions of the petriotic ventrally.

Anterior to the aperture in the petrosal where the facial nerve emerges there is a deep, anteroposteriorly elongate fossa the roof of which covers the facial canal ventrally and which continues anteriorly after a short hiatus, presumably for a branch of the stapedial artery, with the broad groove in the alisphenoid for the eustachian tube. This fossa would also house the tensor tympani muscle. Lateral to this fossa and partially ventral to it there is a broad exposure of the mastoid near, and occasionally adjacent to, the postglenoid foramen. This exposure of the mastoid, anterodorsal to the position of the audital tube must have been about where the anterior leg of the tympanic annulus made contact. It is immediately behind the posterior margin of the crest or pedicle formed of the squamosal and alisphenoid suspected of supporting a bulla.

The lateral wall of the mastoid, when the squamosal covering is removed posterodorsal to the above exposure adjacent to the audital tube, shows a deeply intrenched, nearly circular, and occasionally branching path for the venous sinus terminating in the postglenoid foramen. It is interesting to note that the lower arc of this sinus, directly above the position of the external auditory meatus, appears to be less curved in small *M. chamense* than in *M. robustum*, as observed in two individuals of each.

The dorsomedial surface of the petiotic shows a relatively large internal auditory meatus, directly opposite the promontorium on the ventrolateral surface. Above the horizontal superior rim of this opening is a large, obtuse conical depression for the flocculus of the cerebellum. At the apex of this conical surface in its posteroventral portion there would appear to be a foramen of variable size. Possibly this is the aqueductus vestibuli, but this may be located in a more customary position directly posterior on the rim or crest of the floccular fossa, where there also seems evidence for a foramen. On the broad posteroventral margin of the petrosal, posteroventral to the internal auditory meatus is a very large aperture which inward is reduced to a rather small foramen that may well be the aqueductus cochleae. The hiatus Fallopii for the superficial petrosal nerve is evidently at the anterior apex of the petrosal.

The petrosal seems relatively small in *Phenacodus*, the actual size in large *P. primaevus* being only a little greater than in *M. robustum*. It is clearly a little thicker and broader through its mid-section, but its length to the anterior apex is relatively less. The general plan of the ventrolateral surface is rather alike in the two, with the position of the fenestrae and the details of the facial canal and sulcus being not greatly different. The aperture of the facial canal, however, is situated a little deeper anterodorsal to the fenestra ovalis; also the hiatus Fallopii, rather large in one of the two specimens examined, is located more medial to the apex, rather than at the apex as observed in *M. chamense* skulls. In the posterior portion the fenestra rotunda is more widely separated from the foramen lacerum posterius, and the facial sulcus swings around more posterior to this fenestra as it turns more gradually downward in *Phenacodus*.

The inner or dorsal surface of the petrosal in *Phenacodus* shows no striking differences, with the internal auditory meatus large and similarly placed. The aqueductus cochleae shows the same wide aperture to a small foramen but is possibly a little more dorsal along the posterior margin. The aqueductus vestibuli seems decidedly slit-like at the posterior margin of the dorsomedial surface, entering the posterior part of the crest which defines the lower margin of the floccular fossa. In the material at hand I was unable to determine the presence or absence of a foramen in the depth of the floccular fossa noted in *Meniscotherium*.

The petrosal in *Hyopsodus* appears long and slender in ventral view, as a slender cone with its apex directed forward and medially.



The promontorium is not separately defined. The relatively large fenestra rotunda faces backward, outward, and downward. Its posterior rim is joined by a crest from the medial portion of the ventrally exposed mastoid which also forms an anterior root of the paroccipital process. This crest at the posterior rim of the fenestra rotunda may also have supported a tympanohyal. Posteromedial to the fenestra rotunda and anteromedial to the paroccipital process is a comparatively large foramen lacerum posterius. The relations here are closely similar to those in *Meniscotherium*. Anterodorsal to the fenestra rotunda is the smaller outward-facing fenestra ovalis. As in *Meniscotherium* the facial nerve would emerge from an aperture anterodorsal to the fenestra ovalis, descend to a position opposite the fenestra ovalis, turn backward then downward to appear anterolateral to the root of the paroccipital process, were the otic area covered by a bulla.

The medial margin of the petrosal in *Hyopsodus* shows a broad longitudinal groove partially formed by the lateral margin of the basioccipital. The posterior extremity is determined by the point at which the petrosal more solidly abuts the basioccipital, closer to the foramen lacerum posterius than in *Meniscotherium*. This groove clearly opens into the cranial cavity medial to the anterior extremity of the petrosal and no doubt carried the internal carotid as interpreted for *Meniscotherium*.

The dorsomedial surface of the petrosal could not be seen in any of the *Hyopsodus* material at hand without damage to the specimen.

#### ENDOCRANIAL CAST

An endocast of *Meniscotherium* was briefly mentioned by Edinger (1956, p. 17) as being much smaller than that of *Phenacodus* but of the same type. In addition to the specimen that she examined (fig. 2, A.M. 48082), there are at hand two casts in the collections of the U. S. National Museum. One of these (fig. 3, U.S.N.M. 23113) is a natural but somewhat eroded cast which includes the rostral as well as the cranial portion. The other (fig. 4, U.S.N.M. 19509) was prepared in rubber from assembled cranial fragments, but includes essentially only the dorsal surface, as its ventral surface is incomplete posterior to the olfactory bulbs. Cranial fragments of various other specimens present detail in restricted areas.

The endocast of *Meniscotherium*, though actually smaller than in *Phenacodus*, is relatively larger, as observed by Cope (1884b, p. 494). It appears elongate and slender, noticeably in the area of the



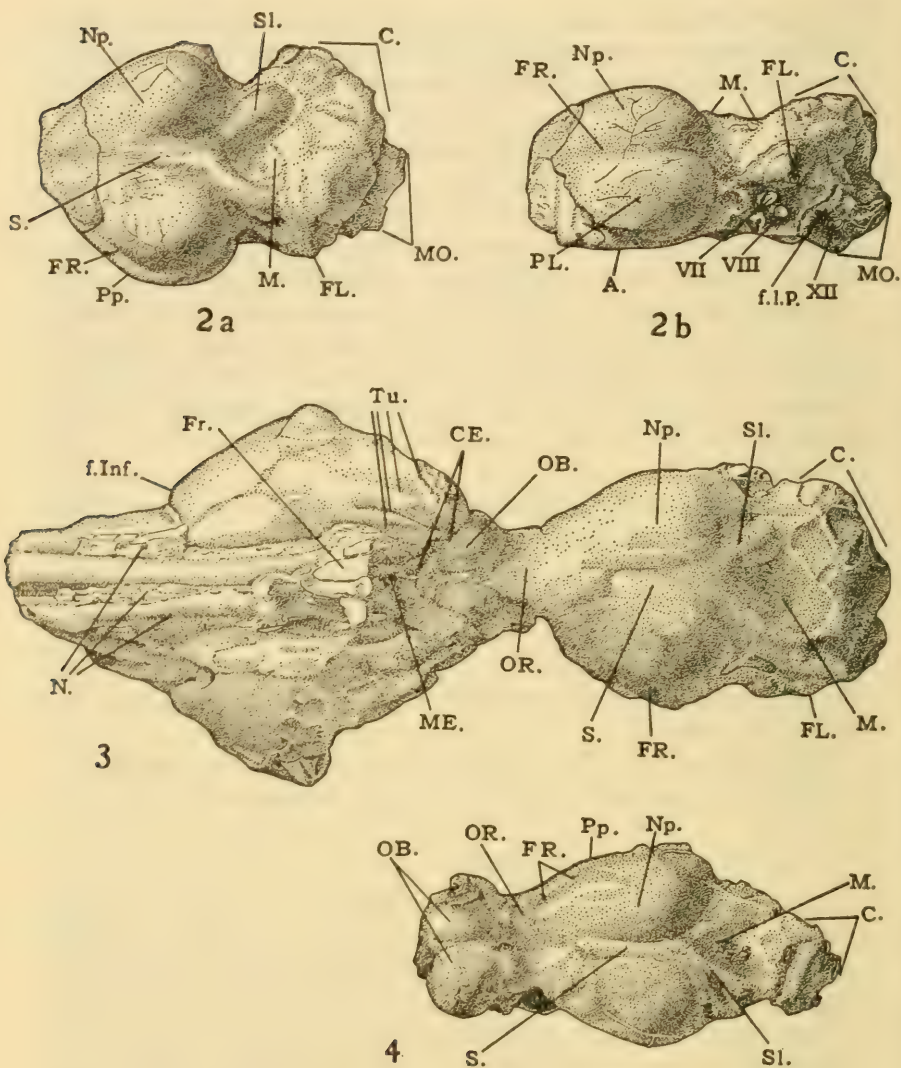


FIG. 2.—*Meniscotherium chamense* Cope. Natural endocranial cast (A.M. 48082); a, dorsal view; b, lateral view of left side. Natural size.

FIG. 3.—*Meniscotherium robustum* Thorpe. Natural endocast of skull (U.S.N.M. 23113), dorsal view. Natural size.

FIG. 4.—*Meniscotherium robustum* Thorpe. Endocast of cranial roof (U.S.N.M. 19509), dorsal view. Natural size.

For explanations see opposite page.

olfactory bulbs and their roots or peduncles, and particularly more slender across the pyriform lobes. It may, however, have been a little less elongate in the cerebral portion than in *Hyracotherium*, as the latter was figured by Edinger (1948, fig. 2). It seems, however, to have reached a rather similar stage of development.

The olfactory bulbs as seen in the rubber mold are distinctly less divergent than in the *Phenacodus* cast and dorsoventrally less compressed. There is a longitudinal fissure separating the lobes on the dorsal surface, but which seems much less deeply impressed than on the ventral surface. Moreover, on the ventral surface this fissure is much less wide open and does not extend posteriorly dividing the olfactory peduncles as it does in *Phenacodus*. In *Meniscotherium* the ventral surface of the olfactory roots shows a gentle concavity, which changes to a gentle convexity posteriorward, and a slight longitudinal ridge on the mold—the trace of the suture between the orbitosphenoids—extends posteriorward from near the fissure between the olfactory bulbs to the optic chiasma. In the *Phenacodus* cast the deep fissure extends almost to the chiasma.

The neopallium in *Meniscotherium* is moderately elongate and

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Explanation of figures 2-4

A., Ridge representing groove, possibly the cavernous sinus, and may have contained nerves III, IV, V<sub>1-2</sub> and VI.

C., Cerebellum.

CE., Cribiform plate.

FL., Flocculus.

f.Inf., Position of infraorbital foramen.

f.l.p., Filling of foramen lacerum posterius.

FR., Rhinal fissure.

Fr., Remnant of frontal bone.

M., General position or covering of midbrain.

ME., Mesethmoid.

MO., Medulla oblongata.

N., Remnants of inferior crests of nasals.

Np., Neopallium.

OB., Olfactory bulb.

OR., Olfactory root.

PL., Pyriform lobe.

Pp., Paleopallium.

S., Sagittal or longitudinal sinus.

Sl., Lateral sinus.

Tu., Impressions of turbinals.

VII., Position of facial nerve in internal auditory meatus.

VIII., Position of auditory nerve in internal auditory meatus.

XII., Filling of hypoglossal or condylar foramen.

tapers forward to anterior poles nearly at the narrows of the olfactory peduncles but well separated from the olfactory bulbs. The cerebral hemispheres would seem comparatively smooth or lissencephalic, suggesting that there were no gyri or sulci, although such, if weakly developed, might have been obscured by the dura mater. There is, however, a slight depression on the dorsolateral surface in the forward portion on either side of the rubber mold, in a position of a sulcus suprasylvius, although it is not a true sulcus or furrow. The fissure rhinalis is clearly defined in all specimens, and it is seen that the neopallium is a little less than half the depth of the endocranial cast as seen in lateral view. The cerebral hemispheres are rather widely separated along the midline, and the impression of the longitudinal or sagittal sinus made on the endocranium is clearly shown. Posteriorly this sinus divides, and the two branches or lateral sinuses diverge obliquely across the space above the midbrain. In their position relative to the midbrain one is tempted to speculate on the possibility of these branches representing instead the corpora quadrigemina, but their direct continuity with the sagittal sinus makes this seem highly improbable. It is interesting to note that at the confluence of the lateral sinuses with the sagittal sinus the right branch invariably leaves the union at a somewhat lower level than the left. The marked size of these structures on the casts, moreover, suggests the importance of these veins in *Meniscotherium*. In *Phenacodus* the cast does not include the form of the sagittal and lateral venous sinuses above.

The cerebellar portion is very poorly preserved in all the casts, but there is evidence that it did not rise as high as in *Phenacodus*. The lateral surface in both natural casts, nevertheless, shows the impression of the petrosal. The small pedicle representing the internal auditory meatus is distinct, and in one cast (A.M. 48082) its apex shows the division into positions of the facial (above) and auditory (below) nerves. Above this, representation of the flocculus of the cerebellum shows the askew conical form, discussed above under description of the petrosal, with its somewhat extended apex directed posteroventrally.

Unfortunately, none of the endocasts of *Meniscotherium* shows much detail on the ventral surface. Both of the natural casts, however, show a generally rounded pyriform lobe, extending outward a little beyond the neopallium, but much less inflated laterally than in *Phenacodus*, possibly indicating a better developed sense of smell in the latter. Immediately medial to the pyriform lobe is seen a very



prominent, elongate and broadly rounded ridge (A. on fig. 3b) on both of the natural casts, corresponding in a general way to the space above the broadly expanded bulge at the posterior root of the pterygoid wing of the alisphenoid. It is not complete anteriorly in either specimen but no doubt terminated anteromedially at the sphenoidal fissure in the endocranium. The margins of this crest are obscure so that details of division or possible branching are not evident, and stalks for the various orifices are not preserved, but in its posterior direction it turns definitely upward and outward behind the pyriform lobe and adjacent to the apex of the petrosal. Because of its gross size, I suspect that its total representation may be rather complex, and in addition to the nerves III, IV, V<sub>1-2</sub>, and VI forward, it possibly represents a cavernous sinus connecting with the ophthalmic vein forward through the sphenoidal fissure and with a petrosal sinus or sinuses posteriorward behind the pyriform lobe. Posteriorly, as far as can be ascertained, its position also conforms with the point of entrance for the internal carotid posteromedially and with the position of the foramen ovale ventrolaterally where the third branch of the trigeminal would emerge.

On one of the casts a small portion of the surface representing the medulla oblongata is preserved around the lower and left side, and on the lower surface, very close to the lateral margin of the dorsoventrally compressed lateral portion, the position of the hypoglossal or condylar foramen is clearly defined. A short distance anterodorsal to this, at the posteroventral margin of the surface formed by the petrosal is a short slightly curved ridge which denotes the cranial opening of the foramen lacerum posterius.

#### MANDIBLE

The most noticeable features of the lower jaw of *Meniscotherium* are the increase in depth of the inferior ramus posteriorward and the extraordinary fanlike posterior extension of the angle (see pl. 3). The two jaws are strongly united by an elongate symphysis which below its posterior margin leaves a broad surface or pit for the digastric muscle. The importance of this muscle has been attested by the previously mentioned prominence of the paroccipital process. Close to the symphysis on the anteroventral surface of the mandible are a pair of foramina rather close to the roots of the 1st incisors. The anterior of the two mental foramina is located below the first premolar or the space between P<sub>1</sub> and P<sub>2</sub>. The second mental foramen is rather generally situated low beneath P<sub>4</sub>. The inferior dental fora-



men is high on the medial surface, a little below and a short distance posterior to  $M_3$ .

The extensive breadth and depth of the angle of the lower jaw indicates a large area of attachment for the masseter muscle externally and the internal pterygoid muscle medially. These, of course, correlate with the depth and strength of the zygoma and the prominence of the pterygoid fossa, and are important in the lateral movement of the jaw for grinding as well as in raising it. The masseteric fossa, however, is not deeply excavated, and its forward boundary is very weakly defined. Dorsally a weak ridge extending upward and backward from the anterior margin toward the sigmoid notch would seem to distinguish between the areas of the masseter and temporal muscles.

The anterior margin of the ascending ramus rises abruptly and high to the dorsoventrally elongate and slightly backward curving coronoid process. The coronoid process is not wide anteroposteriorly, and the sharp sigmoid notch is followed immediately by the generally convex and decidedly oblique condyle. The condyle has very little neck and is situated well forward with respect to the posterior margin of the angle.

The lower jaws of other Eocene condylarths do not generally taper forward so markedly through their length as in *Meniscotherium*, although in some specimens of *Hyopsodus* the increase in depth posteriorly was rather noticeable. The depth of jaw in *Phenacodus* and *Ectocion* is relatively less and seems more nearly uniform beneath the cheek teeth. In all these the jaws are strongly united at the symphysis although the symphysis may not extend so far posteriorly with respect to the cheek teeth as in *Meniscotherium*. Moreover, although *Phenacodus* shows a rather prominently expanded angle, it seems relatively less so than in *Meniscotherium*. Also, the masseteric fossa is more noticeably excavated in all and better defined anteriorly than in *Meniscotherium*. In a relatively well preserved mandible of *Hyopsodus* it was observed in addition to the well-excavated masseteric fossa that the coronoid process seems relatively broader anteroposteriorly and not so high, also that the condyle has its long axis distinctly transverse and is a little less convex across this diameter.

The mental foramina in *Phenacodus* appear generally to be two in number and placed about beneath  $P_1$  and  $P_4$ . This would appear to be the case also for *Ectocion* in the limited material at hand. In *Hyopsodus*, however, there are frequently, if not generally, three and sometimes four foramina spread out between a position beneath  $P_1$  to  $P_4$  or  $M_1$ .

## DENTITION

*Upper dentition.*—Although the cheek teeth of *Meniscotherium* (see pl. 5) are surprisingly precocious in having very early reached a high degree of selenodonty for a condylarth, and the molarization procedure having already extended forward to include the fourth premolar by the beginning of the Eocene, the more anterior teeth are decidedly unspecialized and little differentiated.

The incisors are basically simple, single-cusped teeth, but subspatulate in that high medial and lateral crests are developed. They approximate the form of very simple premolars with the shorter anterior (anteromedial) crest deflected medially at its anterior extremity and the longer posterior (posterolateral) crest straight and with a steeper slope, especially I<sup>3</sup>, which may exhibit an incipient lateral cuspule. These teeth may be about the same size or increase slightly to I<sup>3</sup>.

The canine is only slightly larger and follows the incisors with essentially no diastema. Its crown is a little higher and the anterior and posterior crests are more subdued and steeper. It evidently functioned more as an extension of the incisor series.

The only diastemata in the rather closely continuous tooth sequence are the short intervals that separate P<sup>1</sup> from the canine and P<sup>2</sup>. P<sup>1</sup> is a very simple tooth about the size of the third incisor but with the anterior crest more steeply sloping, as in the somewhat larger canine. P<sup>1</sup>, however, has two roots, although these may not be completely divided.

P<sup>2</sup> is appreciably larger than P<sup>1</sup> and relatively much broader across the posterior root. This tooth is highly variable and in some specimens its crown structure is as simple as that of P<sup>1</sup> but with a stronger posterior crest, whereas in others of the same species there may be developed a posterointernal rugosity to a clearly defined deutocone with accessory cuspules.

P<sup>3</sup> is about intermediate in size between P<sup>2</sup> and P<sup>4</sup> and invariably exhibits a well-developed, conical deutocone (protocone). This tooth seems highly variable with regard to the development of a tritocone (metacone), and when the latter is fairly well defined, although invariably less prominent than the primary cusp, there may be a very weak, posteriorly placed mesostyle. A small cuspule in the position of a tetartocone (hypocone) is invariably present on the cingulum posterolateral to the deutocone. A similar cuspule symmetrically placed anterolateral to the deutocone seems invariable and arises from the anterior cingulum when the latter is developed.

In the anterior part of the small median valley a protoconule, isolated from the anterior cingulum and often from the deutocone, is attached to the lingual wall of the primary cusp. The metaconule, in the posterior part of this valley, as a crest may join the deutocone and the tritocone portion of the outer wall but is usually separate from the posterior cingulum or tetartocone in this tooth.

P<sup>4</sup> is distinctly more molariform than P<sup>3</sup>. The deutocone is very large and conical, and the tritocone, while usually somewhat more abbreviated than the primary cusp (paracone), is well defined. The mesostyle may be fully developed but this is not invariable, as in some specimens it is no more than a gentle swelling or flexure of the outer wall and somewhat nearer the posterior margin than in the molars. The ribs, moreover, are a little better defined than in the molars. P<sup>4</sup> is most noticeably different from the molars in the much less lingual position of the tetartocone, which appears more as a cusp on the posterior cingulum, but is strongly joined to the metaconule, and the latter generally shows little or no direct union with either the deutocone or tritocone. The protoconule forms a short crest parallel to the anterior crest of the primary cusp which it joins posteriorly. This accessory cuspule may also be joined, but somewhat more weakly, by a crest from the deutocone. The cuspule on the anterior cingulum anterolateral to the deutocone persists as in the molars, as well as in P<sup>3</sup>. Slight plications extending into the central basin from adjacent cusps and walls were noted in certain of the fourth premolars, but this condition was less frequently encountered here than in the molars.

The first two true molars may be discussed together as they are much alike except for the greater size of M<sup>2</sup>. The outer walls of these teeth show exceedingly well developed parastyles and mesostyles, and with but feeble or no representation of ribs in the concavities corresponding to the outer walls of the paracone and metacone. The protocone is conical but somewhat more elongate toward the protoconule than is the deutocone of P<sup>3</sup> and P<sup>4</sup>. The hypocone is completely lingual in position and forms with the metaconule an elongate ridge extending anteroexternally well into the central pit or valley of the tooth. Also the posterior cingulum rises lingually and prominently to the crest of the hypocone giving this cusp a crescentic or V-shaped appearance. The anterior cingulum usually extends around the base of the protocone, terminating in the valley between the protocone and hypocone. It carries a prominent cuspule antero-external to the protocone as observed in P<sup>3</sup> and P<sup>4</sup>. The proto-



conule is crescentic, paralleling the paracone, and its posterior limb joins the inner wall of the paracone toward the center of the tooth. There is, moreover, rather generally a highly variable complex of plications extending from paracone, metacone, protoconule and metaconule into the median pit or valley of these two teeth.

M<sup>3</sup> differs from the preceding molars in the narrower talon portion, with the much less lingual position of the hypocone and the shorter crest that this cusp forms with the metaconule. The lingual portion of M<sup>3</sup> is surprisingly like that of P<sup>4</sup>. The development of the external crests and styles, however, immediately distinguishes these teeth.

*Lower dentition.*—The lower incisors also appear comparatively simple, although I have been unable to observe any in a completely unworn state. They are much more procumbent than in the premaxilla and exhibit longer and nearly straight roots. They are comparatively small with an anteroposteriorly compressed crown, and I<sub>2</sub>, often the largest of the three, shows a more triangular wearing surface. The root portion of the second incisor may also have broader forward and somewhat more compressed (transversely) posterodorsal portion. I<sub>3</sub> is larger than I<sub>1</sub> but may not always equal I<sub>2</sub> in size and is rarely larger. Its wearing surface is oval in outline.

The canine has a stronger root than the incisors and is closely appressed to the third. Its crown, while tapering somewhat upward, shows a high but relatively short anterior crest which wears much as the third incisor. Its weak or subdued posterior crest is steeply sloping and may exhibit an incipient cuspule or small buttress at its base.

P<sub>1</sub>, single rooted, has a crown much like that of the canine, although smaller and transversely more slender. P<sub>2</sub> may be single rooted or double rooted, and in the latter instance the roots may not be completely divided. It is a little larger than P<sub>1</sub>, and its crown though likewise simple is relatively lower and anteroposteriorly more elongate with a longer anterior crest and usually a somewhat better defined buttress at the base of the posterior crest. Very short diastemata may separate this tooth in the series although occasionally P<sub>1</sub> is the isolated tooth, or still shorter diastemata may tend to isolate both.

P<sub>3</sub> is double rooted and much larger than the preceding premolars. The anterior crest, while somewhat variable in length and height, always shows a marked medial flexure anteriorly, some specimens exhibiting a distinct paraconid. The posterior crest is well defined,



and its lower extremity forms a high median crest on a usually broad and well-developed talonid.

P<sub>4</sub> is quite molariform and differs from the anterior molars essentially in the relatively longer and somewhat narrower trigonid portion with its more widely open crescent. This anterior crescent may also show somewhat better evidence of a distinct paraconid than in the molars. Also, the posterointernal extremity of the posterior crescent may be more medial and often shows an extra cusp.

The first two molars, as in the upper series, are much alike with M<sub>2</sub> noticeably larger. They are highly selenodont with the posterior or talonid crescent a little more elongate anteroposteriorly than the anterior or trigonid crescent, and the outer walls of the crescents are more hypsodont than the inner walls. The anterior crest of the trigonid is somewhat recurved posteriorward at its lingual extremity but is not raised to form a definable paraconid. The metaconid and entoconid (or hypoconulid?), however, are well defined and relatively high in unworn teeth. The anterior crest or crista obliqua of the hypocone joins the anterior crescent at the metaconid a little below its apex, and on the posterior slope of this cusp there is almost invariably a well-developed and somewhat lingually flexed meta-stylid crest which may show a distinct cuspsule. This tends to constrict the talonid basin lingually and there may also be a small extra cuspsule at the mouth of the valley or basin.

M<sub>3</sub> differs from the anterior molars only in that the talonid portion is a little more elongate and slightly narrower. Moreover, there is a buttresslike extension or crest on the posterior wall of the entoconid (or hypoconulid?). The greater length and narrower talonid portion is a development just the reverse of that observed in P<sub>4</sub>.

*Deciduous upper premolars.*—Dp<sup>3</sup> is a rather distinctive tooth in the upper series, and while it seems to show somewhat the same detail as P<sup>3</sup>, it is very much askew with the talonid portion deflected decidedly posterolingually rather than having the nearly symmetrical appearance of the permanent tooth. Moreover the small cuspsules anteroexternal and posteroexternal to the deutocone are very weak or missing, whereas the outer wall shows a rather prominent development of a style at the anterior extremity and the tritocone is better defined than in P<sup>3</sup>.

Dp<sup>4</sup> is almost indistinguishable from M<sup>1</sup> except for its smaller size and greater wear, when found associated with it. It does, however, show a relatively more forward position for the parastyle, and occasionally the tooth is a little more askew than M<sup>1</sup>. It is, of course,

readily distinguished from  $P^4$  by the development and lingual position of the tetartocone (hypocone).

*Deciduous lower premolars.*— $Dp_3$  is much like  $P_3$  but appears to be a little more complex. The anterior crest seems more crescentic and its anterolingual extremity is sometimes bifurcate or plicated lingual to the paraconid. Also, in addition to the median posterior crest which is much as in the permanent tooth, rather prominent crests extend down the posterolingual and posterolateral slopes of the protoconid nearly to the talonid.

$Dp_4$  is almost indistinguishable from  $P_4$  but is a trifle more elongate in both the trigonid and talonid portions. Also, the anterointernal extremity of the trigonid crescent is generally not recurved but there is often a sharply angular flexure or style essentially comparable to and paralleling the metastylid crest. In some  $Dp_4$ 's the anterior extremity of this crest appears essentially bifurcate, almost as in  $Dp_3$ . The deciduous fourth premolar is also distinctly lower crowned than the permanent premolar.

#### VERTEBRAE

Although ribs are rather poorly preserved in the available skeletal portions of *Meniscotherium* and show very little of interest, which also may be said of the sternal material, significant segments of the vertebral column are included in at least three individuals, two representing *M. chamense* and one of *M. robustum*.

*Cervical vertebrae.*—The atlas vertebra is decidedly short anteroposteriorly, perhaps more so than in *Phenacodus*, and the transverse processes are not widely expanded, although they appear to be a little more extended than in the larger form. They rise anteriorly, and just ahead of and above the anterior extremity on each side the large foramen for the first spinal nerve is completely enclosed, opening into the neural canal just posterior to the upper extremity of the facet for articulation with the occipital condyle. A decidedly large vertebrarterial canal opens forward on the inferior surface of the transverse process and has its posterior aperture on the deeper posterior margin of the transverse process, just lateral to the widest part of the facet for the axis. These foramina appear to be very much like those in the *Phenacodus* atlas illustrated by Cope (1884b, pl. 57h) although relatively larger.

The axis is much the longest vertebra in the neck and broadest across the ventral surface of the centrum. The spinous process is moderately high and relatively elongate anteroposteriorly but evi-

dently is not extended posteriorly so much as in *Phenacodus*. The transverse processes are slender and curve sharply backward and are pierced anteroposteriorly, close to the centrum, by a large vertebrarterial canal on each side. The anterior aperture of the canal is immediately posterior to, and somewhat recessed behind, the outward flaring lateral margin of the atlantal facet or surface. The odontoid process is stout and nearly cylindrical.

The succeeding cervical vertebrae decrease in length posteriorly with the centra somewhat flattened dorsoventrally and with surprisingly large and relatively broad neural canals. The breadth of the neural arch dorsally is evident in the transversely wide spacing of the zygapophyses. The transverse processes extend prominently outward



FIG. 5.—*Meniscotherium chamense* Cope. Cervical and anterior dorsal vertebrae (U.S.N.M. 22672); a, lateral view; b, ventral view.  $\frac{1}{2}\times$  natural size. New Fork member, Wasatch formation, Green River Basin, Wyo.

and downward from essentially the anterior half or two-thirds of the centrum, the sixth cervical showing the characteristic posterior extension or expansion of the inferior lamella. The vertebrarterial canal, as in the atlas and axis, is a conspicuously large foramen in all except the seventh which, lacking the inferior lamella, may show a broad groove on the lower surface of the transverse process close to the centrum. The spinous processes are low on the third to about the sixth cervical, but the seventh shows some elongation and a slight backward tilt. The inferior surfaces of the centra are comparatively broad and flat without hypapophyses (see figs. 5 and 6), although the axis to the fifth cervical shows a low keel which posteriorly on each broadens into a triangular flat hypapophysial table, as noted by Cope (1884b) for both *Meniscotherium* and *Phenacodus*. Also, as



noted by Cope, the centra are slightly opisthocoelus and the articular surfaces distinctly oblique.

*Dorsal vertebrae.*—The number of dorsal vertebrae in *Meniscotherium* is not known, although it was probably close to that of *Phenacodus* which was given by Cope as 14 or 15. In one of the articulated series at hand (see fig. 5) only the first seven are preserved in place and in another the last six. These show a decrease in size from the cervicals, but there is a surprising increase in size near the posterior limit of the sequence and into the lumbar. The anterior dorsals are only slightly shorter than the cervicals but noticeably narrower across the zygapophyses and the centra are dorsoventrally flattened. The neural spines, after the first, are rather slender and



FIG. 6.—*Meniscotherium robustum* Thorpe. Cervical and anterior dorsal vertebrae (U.S.N.M. 18283); a, dorsal view; b, ventral view.  $\frac{1}{2}\times$  natural size. Knight member, Wasatch formation, Green River Basin, Wyo.

backward directed in the anterior part of the series, but posteriorly they become shorter, more erect, and anteroposteriorly wider, with the last one or two tilting forward. The transverse processes carrying the articular surface for the tubercle of the rib are markedly elongate, at least in the first seven, and rudimentary metapophyses extending upward from the transverse processes above the tubercle facet, although mostly damaged, are evident. Posteriorly the facet for the tubercle of the rib is supported by more of a pedicle extending antero-ventrally from the transverse process, and the metapophysis becomes better defined and separate from both. In the fourth from the last dorsal the three structures are joined in a common base, and the



anterodorsally and laterally directed metapophysis is much larger than the feeble posteroventrally and outwardly directed transverse process. In the succeeding dorsals the rib has but a single articulation, with the margin of the centrum, and the higher metapophysis has moved up closer to the anterior zygapophysis and is completely separate from the still shorter transverse process. In the last couple of dorsals, in addition to the increasing size and relatively greater depth of the centrum for this portion of the series, the metapophyses are broadly expanded and the transverse processes are much reduced. There are no anapophyses in the sequence, and in no instance was the intervertebral foramen found to be completely closed by the pedicle of the arch.

*Lumbar vertebrae*.—A lumbar series for both *M. chamense* and *M. robustum* is included in the collections (see figs. 7 and 8). The number is nine in the *M. chamense* skeleton, and the nine articulated presacrals preserved in the *M. robustum* skeleton all seem to be

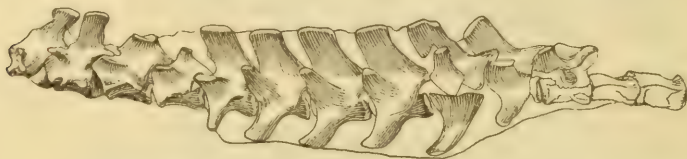


FIG. 7.—*Meniscotherium chamense* Cope. Lumbar and four posterior dorsal vertebrae (U.S.N.M. 22918), lateral view of left side.  $\frac{1}{2}\times$  natural size. New Fork member, Wasatch formation, Green River Basin, Wyo.

lumbar. Cope considered that *Phenacodus* had six or seven lumbar, but there seem to be only four or five in the *Phenacodus primaevus* skeleton that I examined. These vertebrae in *Meniscotherium* are seen to be extraordinarily large in comparison with the greater part of the dorsal series. The forward sloping spines and transverse processes increase in length posteriorly, at least as far as the sixth, and these appear relatively broader anteroposteriorly in the larger of the two species. The processes of the more posterior lumbar are poorly preserved in both specimens. The metapophyses, beginning with their separation from the transverse processes near the end of the dorsal series, increase in height and strength to about the fifth or sixth lumbar, and posteriorly become subdued with little or no projection beyond the margin of the anterior zygapophyses. Laterally the zygapophyses in the lumbar series turn decidedly upward, beyond which the metapophyses continue upward as well as outward and

forward. The ventral surface of the centrum is broad and only moderately keeled.

*Sacrum.*—The sacrum includes four well-coalesced vertebrae which



FIG. 8.—*Meniscotherium robustum* Thorpe. Lumbar and sacral vertebrae, and pelvic girdle (U.S.N.M. 18283, ilium restored from U.S.N.M. 19555); a, dorsal view; b, ventral view.  $\frac{2}{5}\times$  natural size. Knight member, Wasatch formation, Green River Basin, Wyo.

ventrally appear to have about the same length each as the lumbar. Cope considered that the number of sacral vertebrae was three, but his specimen may have been incomplete. Certainly Marsh's sacrum of "*Hyracops socialis*" with four sacrals does not differ from the

normal in *Meniscotherium*. For *Phenacodus* Cope listed the number as three or five. His illustration (1884b, pl. 57h) shows four.

Anteriorly the fused transverse processes, preserving nevertheless the intervertebral foramen, show a strong and deep attachment to the ilium. The anterior spines are not preserved, but the posterior two, although incomplete, were evidently low and backward directed.

*Caudal vertebrae*.—There are 14 caudal vertebrae (see fig. 9) belonging to one specimen, but most of these were not found articulated, so that any sequential arrangement of these would likely be very incomplete. The first caudal is in articulation with the sacrum described above. Although a little shorter, it is nearly as large as the last sacral and has heavy, laterally directed transverse processes. Posteriorly the caudals become a little shorter as well as smaller in

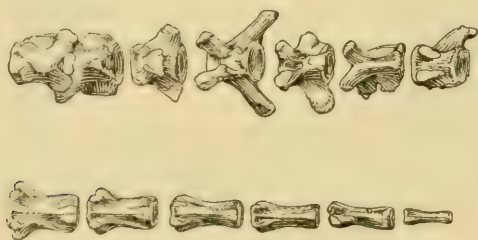


FIG. 9.—*Meniscotherium robustum* Thorpe. Caudal vertebrae, not an articulated series (U.S.N.M. 18283), dorsal view.  $\frac{1}{2}\times$  natural size. Knight member, Wasatch formation, Green River Basin, Wyo.

diameter than the first, with more slender, shorter, and backward directed transverse processes. After about the eighth of those at hand their length increases again and the processes and pedicles are reduced to vestiges. Only the first four or five of those represented show evidence of a neural spine, and the anterior caudals lack a distinct ventral keel, but posteriorly the latter is better defined.

#### SCAPULA

The scapula of *Meniscotherium* is relatively elongate and, although in the one well-preserved example at hand (see pl. 6) the margins are not everywhere complete, the suprascapular border would appear to be rounded somewhat as in *Phenacodus*, but the coracoid or anterior border may not expand forward so abruptly near the proximal extremity. The prescapular fossa is distinctly convex and, as in *Phenacodus*, is much wider than the postscapular fossa. The latter is



highly concave anteroposteriorly and the glenoid or posterior border is turned sharply outward. The concave glenoid surface is nearly oval but somewhat compressed or acuminate at the proximally directed anterior extremity. The coracoid process here exhibits a strong medially deflected flange or hook which is separated from the glenoid surface by a distinct groove or notch, much as described by Cope for *Phenacodus*.

The most striking feature of the *Meniscotherium* scapula is the very high but posteriorly deflected spine with its prominent antero-proximally directed acromion and strongly recurved but posteriorly directed metacromion. The spine apparently maintains nearly its maximum height from the acromion to about its midpoint and distally from there it tapers to the suprascapular border. The spine was evidently broken off the various scapulae of *Phenacodus* available to Cope, but an equivalent development of the acromion and metacromion was observed on the *Phenacodus* skeleton exhibited at Princeton University.

There is apparently no evidence for a clavicle in either *Meniscotherium* or *Phenacodus*.

#### HUMERUS

The limb bones of *Meniscotherium* appear to be relatively a little smaller, in proportion to the size of the skull for example, and somewhat less robust than in *Phenacodus*. The humerus (see pls. 6 and 7) is slender and gently curved, more noticeably in the smaller *M. chamense*, but shows, nevertheless, a prominent and elongate deltoid ridge extending from two-thirds to nearly the entire length of the shaft, giving the proximal portion of the shaft a somewhat flattened (anteromedial-posterolaterally) appearance (see Cope, 1884b, pl. 25g, fig. 12). The development of this crest together with the height of the spine and development of the acromion on the scapula testify to the importance and leverage afforded the deltoid muscle in abducting the forelimb. The proximal portion of the humerus is characterized also by a prominently projecting crestlike greater tuberosity, whereas the lesser tuberosity shows very little proximal projection, although its medial prominence exhibits a noticeable dorsomedial facet or scar for the subscapularis muscle. The tuberosities are separated by a broad bicipital groove but are closely joined to the head, leaving little or no anatomical neck. Cope (1884b, p. 502) noted that there were no bicipital ridges, but these may be weakly developed on some specimens. He also described a *teres*



major ridge as distinct and extending on the proximal two-fifths of the length. This I find, however, is variable and usually weak or absent but noted it observably developed on two specimens of *M. robustum*. There is a generally shallow but well-defined fossa or depression, which may be pitted or nearly flat, on the posterior surface or margin of the greater tuberosity at the proximal extremity of the deltoid ridge, evidently the fossa for the teres minor that Cope mentioned as being flat.

The distal extremity of the humerus is broad with a very well developed inner condyle exhibiting an entepicondylar foramen which is relatively larger in the smaller species *M. chamense*. The inner condyle shows a relatively rough or rugose medial and distal margin for the various flexor and certain other muscles to the manus. The external condyle, however, is not nearly so projecting but is roughly pitted for the extensors. The trochlea has an outstanding medial margin anteriorly and distally and a posteriorly raised lateral margin which arises from the nearly median convexity of the trochlea as it extends around toward the posterolateral side, as noted by Cope. With a posterior root continuous with this posterior lateral crest of the trochlea and with an anterior root originating on the external condyle, a flaring supinator ridge extends prominently upward and somewhat backward for about the distal third of the shaft. Above the trochlea, as noted in several specimens, the bone seems incomplete, leaving usually a broadly open supratrochlear foramen.

The humerus of *Phenacodus* was illustrated by Cope (1884b, pl. 57g, fig. 2) and briefly described. It is surprisingly like that of *Meniscotherium* in a number of details, although it differs noticeably in its generally straighter and relatively somewhat stronger appearance. The proximal tuberosities seem a little more robust and anteriorly more projecting. The bicipital groove is relatively broader and, as Cope noticed, there is a low ridge medially placed in the bicipital groove, which is not seen in *Meniscotherium*. The deltoid and supinator ridges have about the same relative extent as in *Meniscotherium*, but the former crest seems somewhat less sinuous. The distal extremity appears to be less expanded transversely, but the trochlea has relatively greater anteroposterior diameter than in *Meniscotherium*. The details of the marginal crests of the trochlea, however, are somewhat alike in the two forms.

In *Hyopsodus paulus* the proximal extremity of the humerus exhibits much less developed tuberosities. The greater tuberosity is more rounded, less crestlike, and does not extend proximally above the

head, but shows a rounded, well-defined fossa for the *teres minor*. The lesser tuberosity is scarcely more than a scar for the *subscapularis* on the medial side of the head. The distal portion of the humerus is known for *Hyopsodus paulus*, as well as *Hyopsodus walcottianus* (see Matthew, 1915, fig. 10). In both of these the trochlea shows the high anterior crest on the medial margin and the high outer crest extending posteriorly from the median convexity on the anterior surface, quite as in *Meniscotherium*, and possibly more emphasized in *H. walcottianus*. The entepicondylar foramen is present and a broadly open supratrochlear foramen. The greater part of the shaft of the humerus is not preserved in *Hyopsodus* material at hand.

#### RADIUS

The elements of the forearm in *Meniscotherium* are distinctly smaller, relative to the humerus and hind limbs than in *Phenacodus*. This would appear in part to be in keeping with the disparity in size of vertebrae relative to these quarters. The radius (see pl. 7) is decidedly slender proximally but shows a noticeable transverse expansion of the proximal extremity or head for articulation with the humerus. The articular surface is nearly rectangular in appearance with a broad median depression for the anterior convexity of the trochlea, and the internal portion or margin of the surface turns distally in conformity with the forward-extending medial margin of the trochlea. The head of the radius articulates with the ulna at the distal margin of the sigmoid notch, anterolateral to the coronoid process.

The proximal portion of the shaft of the radius may show a rather pronounced groove on its posteromedial surface curving somewhat more medially distally, most noticeable in *M. robustum*. This may well define a portion (fifth) of the origin of the flexor profundus digitorum. Distally the shaft of the radius increases in diameter and curves inward, passing from an anterolateral position proximally to a more medial position distally with respect to the ulna. The posterolateral margin of the distal half of the radius is generally somewhat rugose for attachment of the interosseous membrane. The anterior surface shows a prominent crest arising on the distal half of the shaft and extending distomedially to terminate near the styloid process, and a somewhat more subdued crest terminating anterior to the lateral portion of the distal extremity.

The distal extremity is enlarged and shows two nearly circular, slightly concave facets side by side, the lateral or lunal somewhat the larger, anteroposteriorly. The medial facet for the scaphoid, however, extends a short distance medially over the anteroposterior crest of the styloid process.

The radius in *Phenacodus* resembles that of *Meniscotherium* in the character of the proximal articular surface for the humerus but appears relatively a little deeper anteroposteriorly. However, the shaft is relatively much more sturdy, so that the head does not seem to be so expanded. Distally the shaft is more rounded with less prominent crests than in *Meniscotherium*, and as noted by Cope, the distal portion close to the extremity is enlarged and converges toward the facets for the carpus.

#### ULNA

The *Meniscotherium* ulna (see pl. 7) is decidedly flattened in an anterolateral-posteromedial direction, and a nearly uniform width is maintained from just distal to the sigmoid notch nearly to the distal extremity. The sigmoid notch is markedly convex transversely and, in keeping with the form of the trochlea of the humerus, shows flaring proximolateral and distomedial margins. The olecranon process is anteroposteriorly deep and elongate and shows a rather broad posterior margin, widening proximally and curving somewhat forward to a rugged medially deflected crest for insertions of the triceps group or extensors of the forearm. On the anteromedial surface of the shaft, just distal to the coronoid process there is a deeply impressed and proximodistally somewhat elongate pocket or fossa, presumably for the tendon of the brachialis and clavobrachialis muscles. On the posteroexternal surface of the shaft a prominent median crest arises a short way distal to the sigmoid notch and extends distally toward the posteroexternal margin where it abruptly widens or divides, as noted in *M. chamense*. In the more robust form, however, the broadening of this crest commences more proximally with the anterior margin continuing medially on the shaft. This crest evidently bounds posteriorly the area of attachment or origin for the extensor brevis pollicis. Anterior to the crest the shaft of the ulna is noticeably concave anteroposteriorly. Distally the anteromedial margin of the shaft widens or divides with included space slightly rugose for the interosseous membrane. The distal extremity is broad and usually somewhat flattened, much as the shaft in general. The distal articular surface for the cuneiform is variable but approximately



cylindrical with the long axis parallel to the plane of flattening and distinctly oblique to the long axis of the shaft, extending distally toward the styloid or posterolateral margin.

In attempting to articulate the bones of the fore limb I note that a comparatively prone position for the manus requires that the posterior margin of the ulna be turned decidedly outward and although articulation with the humerus permits appreciable rotation, a relatively normal relationship requires appreciable abduction of the arm.

In *Phenacodus*, as noted above, the ulna is relatively larger and the shaft appears less flattened than in *Meniscotherium*. The proximal portion of the sigmoid notch is very much like that in *Meniscotherium* with a similar transverse convexity and lateral flare, but the distal portion of the surface is much more expanded lateral to the coronoid process so that the head of the radius has a more nearly transverse articulation with the ulna, and a slightly more anterior or ungulate-like position with respect to its humeral articulation. Moreover, this expansion of the sigmoid notch lateral to the coronoid process is accompanied by a proximally more nearly triangular shaft. The robust olecranon in *Phenacodus*, though similar, has a straighter posterior margin or it curves somewhat backward rather than forward as in *Meniscotherium*.

The distal portion of the *Phenacodus* ulna is rather enlarged from the moderately flattened shaft, and the long axis of the distal articular surface for the cuneiform appears more transverse with respect to the flattening of the shaft, seemingly less oblique to the axis of articulation at the sigmoid notch than in *Meniscotherium*.

#### MANUS

As noted with regard to the forearm, the forefoot of *Meniscotherium* (see pl. 7) is relatively much smaller than that of *Phenacodus*; also, the carpals are proximodistally more compressed than in the latter. The carpals, however, show somewhat the same serial arrangement observed in *Phenacodus* but with slightly more overlapping. I was unable to verify the presence of a central in the carpus of *Meniscotherium*, although Marsh (1892, fig. 1) shows this element in the "*Hyracops socialis*" foot that he figured. Slightly more preparation on the specimen (Y.P.M. 10276) that evidently guided Marsh reveals that the prominence in the position of a central is firmly joined to the distolateral angle of the scaphoid and may well be an integral part of that bone. Although this process is variable, it is more prominently developed in the Marsh specimen than in



others at hand and possibly began ossification from a separate center before joining the scaphoid.

*Scaphoid*.—The scaphoid is relatively shortened proximodistally but noticeably elongate in a dorsoventral direction and exhibits a knoblike ventromedial extremity. Displayed across the shorter dorsal portion of the proximal surface, the prominent articular convexity or radial facet extends distad on the dorsal surface nearly to the distal facet for the trapezoid. The distal surface is lunate in outline and the dorsal or anterior portion shows an obliquely oriented concavity for articulation with the trapezoid. Ventromedial to this there is a more flattened to somewhat convex surface for the trapezium. The distolateral angle of the dorsal surface is developed as a small process which may be relatively prominent as discussed above. Ventral from this point a rounded dorsoventral ridge articulates narrowly with the magnum. This ridge divides the concave trapezoidal area medial to it from the small, flattened, dorsally situated, and laterally facing lunar facet immediately proximal to it.

The *Phenacodus* scaphoid as well as being much deeper is distinctly less attenuated ventral to the radial and trapezoidal facets. Moreover, the convexity for articulation with the radius does not extend relatively so far down the dorsal surface as in *Meniscotherium*. The facet for the trapezoid is comparatively flat, and that for the lunar may be small and dorsodistally placed on the lateral surface. There does not appear to be any contact with the lunar unless these may touch at a point ventral to the lunar facet, but evidently not near the dorsal surface of the wrist as in *Meniscotherium*.

*Lunar*.—The lunar in *Meniscotherium* is an arcuate, proximodistally compressed tonguelike structure. It laps dorsoventrally over the proximal hump of the magnum, and its proximal convexity is essentially concentric with its distal concavity. The essentially convex facet for the lateral or lunar facet of the radius covers the entire proximal surface and dorsally approaches the distal surface. Ventral to the median transverse crest this surface is slightly concave before reaching the ventral margin. The concave distal surface is divided for articulation medially and somewhat more dorsally with the magnum and laterally and more ventrally with the unciform. The dorsal portion of the arcuate medial surface of the lunar is faceted for articulation with the scaphoid. The ventral portion of the proximodistally somewhat deeper or less arcuate lateral surface shows a comparatively large facet for the unciform.

The deep, more nodulelike *Phenacodus* lunar has a strongly con-

vex proximal articular surface for the radius, but this does not appear so well faceted farther ventrally nor does it extend relatively so far distally on the dorsal surface. The distal surface for the magnum is more flattened dorsally but exhibits a deep circular concavity on the ventral half for the proximal prominence of the magnum. The more lateral and dorsoventrally concave facet for the unciform faces slightly more laterally and is decidedly narrow and ventrally more restricted than in *Meniscotherium*. Medially the lunar is slightly concave and shows a variably developed facet or facets for the scaphoid. Lateral faceting for the cuneiform is likewise variable and may be restricted to a dorsoventrally elongate zone along the distal portion. The ventral extremity of the *Phenacodus* lunar presents a somewhat more rounded knob; a less-flattened protuberance than in *Meniscotherium*.

*Cuneiform*.—The relatively compressed cuneiform is elongate much as the scaphoid, but its long axis is more nearly transverse with its lateral extremity deflected ventrally. The proximal surface shows a dorsoventrally concave and transversely elongate surface for articulation with the ulna. The relatively acute, transversely elongate ridge that bounds the concavity ventrally divides the ulnar surface from a narrow but transversely somewhat elongate proximoven-tral facet for the pisiform. The facet for the unciform covers the entire transverse portion of the distal surface and is slightly concave dorsoventrally. Transversely a very gentle saddle divides a larger medial portion from a somewhat smaller lateral area. The roughened dorsal surface is distoproximally very shallow laterally but becomes a little deeper medially. The ventral two-thirds of the medial surface is faceted for articulation with the lunar. The ventrally directed lateral extremity is an irregularly flattened prominence that apparently does not support any of the pisiform articulation.

The *Phenacodus* cuneiform is dorsoventrally as well as proximodis-tally deeper relatively, and the ventrally directed lateral extremity is longer and more massive. The ventrolaterally tapering extension or extremity carries most of the large triangular facet for the pisiform on its steeply sloping proximal surface. The concave proximal artic-ular surface for the ulna is approximately as in *Meniscotherium* but relatively deeper dorsoventrally. Also the more uniformly con-cave distal facet for the unciform is dorsoventrally deeper relative to its length transversely. The acutely angled medial surface shows a crescentic facet for the lunar adjacent to the arcuate distal margin.

*Pisiform*.—The *Meniscotherium* pisiform is moderately elongate,

about equaling the greater diameter of the cuneiform. Its articular surfaces are transversely broad but proximodistally shallow, although both increase somewhat in depth laterally. The surface for the ulna is longitudinally concave near the lateral extremity and makes a sharp angle with the more flattened facet for the cuneiform. The shaft of the pisiform is broad proximally but transversely constricted along its distomedial margin. The posterior extremity of the pisiform exhibits an enlarged knob.

In *Phenacodus* the articular extremity of the large pisiform is relatively not so broad transversely, the articular facets are proximodistally deeper, and there is much less of an angle between them than in *Meniscotherium*. The facet for the cuneiform is decidedly triangular, articulating well down on the ventrolateral projection of the cuneiform. The shaft of the pisiform is relatively much deeper proximodistally than in *Meniscotherium* and appears comparatively narrow. The shaft is elongate and terminates posteriorly in a similarly enlarged tuberosity or knob.

*Trapezium*.—The trapezium is broad and proximodistally deep in *Meniscotherium*, and its medial facing surface is comparatively flat. The proximal portion narrows somewhat toward its articulation with the scaphoid, but more distally the dorsal margin is dorsally expanded or flaring, although the ventral margin is nearly straight. The distal extremity exhibits an oval-shaped, slightly concave facet for the first metacarpal. The lateral facing surface has a distinct prominence proximally which supports a narrow but transversely elongate facet on its dorsolateral surface for articulation with the trapezoid, and just below or distal to this a somewhat arcuate surface extends dorsodistally out on the dorsal flare of the trapezium for contact with the base of the second metacarpal.

The *Phenacodus* trapezium appears more nearly rectangular and relatively thicker transversely along the ventral margin. The proximal articular surface for the scaphoid is convex, and that distally for the first metacarpal is concave and somewhat larger. The lateral surface shows pairs of facets proximally and distally for the trapezoid and second metacarpal respectively.

*Trapezoid*.—The trapezoid in *Meniscotherium* is noticeably compressed proximodistally and nearly wedge-shaped with the deepest part at the dorsomedial angle of the bone. The dorsal surface exhibits a prominence distally near the medial margin. The proximal surface for the scaphoid is dorsoventrally convex in the dorsal part but changes to concave in the ventral portion. The distal facet for



the second metacarpal is transversely convex but slightly concave dorsoventrally. It articulates medially by a narrow but dorsoventrally elongate facet with the trapezium but slightly, if at all, with the magnum along its rather thinner lateral margin. It is excluded from contact with the lunar by articulation between the scaphoid and magnum.

The *Phenacodus* trapezoid is not nearly so compressed and presents a quadrilateral rather than nearly triangular dorsal surface. The distal surface for the second metacarpal is similar to that in *Meniscotherium*, but the proximal surface for the scaphoid is more nearly flat. The medial surface exhibits facets for the trapezium, and the lateral surface, unlike *Meniscotherium*, shows a broad crescentic facet for the magnum. There may have been also limited contact with the lunar proximodorsally on the lateral surface, although Cope thought not.

*Magnum*.—The *Meniscotherium* magnum is an irregularly shaped bone relatively narrow transversely and with a proximodistally restricted dorsal exposure. It has a nearly triangular shape in lateral or medial view with the deeper median portion surmounted by a knoblike proximal convexity which with the proximodorsal slope of this triangle articulates with the lunar. Adjacent and parallel to this lunar facet but on the medial surface, the magnum shows a facet for the scaphoid (no central). Along the ventral margin of the medial surface there is an arcuate, slightly concave and elongate surface for the base of the second metacarpal. This surface makes a nearly right angle with the dorsoventrally concave distal surface for the third metacarpal. The entire proximodistal extent of a little more than the dorsal half of the lateral surface articulates with unciform. The ventral part of the magnum is slightly enlarged and extended somewhat beyond the trapezoid and unciform, presumably supporting attachment of a part of the flexor brevis pollicis and possibly certain adductor muscles.

The dorsal surface of the *Phenacodus* magnum is much deeper proximodistally so that the bone does not appear so nearly triangular in lateral or medial view. Also, the surface for the lunar, immediately dorsal to the proximal hump or knob, is more concave. Articulations for the second and third metacarpal and for the unciform are similar to those in *Meniscotherium*, but there may be no articulation with the scaphoid, or it is restricted to a small area on the medial side of the proximal apex. On the other hand, articulation with the trapezoid is rather extensive in the dorsal part of the medial



concavity of the magnum, where there seems to be little or no contact in *Meniscotherium*.

*Unciform*.—The dorsal face of the *Meniscotherium* unciform appears of nearly uniform depth because of the distally extending lip on the lateral half. In ventral view, however, the bone is decidedly triangular with the sloping proximal surface for the cuneiform reaching in a thin lateral margin the facet for the fifth metacarpal. A dorsoventrally convex and transversely narrow facet for the lunar is deflected more medially from the proximomedial margin of the broad surface for the cuneiform. The distal surface is dorsoventrally concave, and a low saddle separates the larger medial surface for the fourth metacarpal from the smaller surface for the base of the fifth metacarpal. The proximal two-thirds of the nearly flat dorsal portion of the deep medial surface articulates with the magnum. The distal margin of this surface articulates with the broad base of the third metacarpal.

The *Phenacodus* unciform is relatively much deeper proximodistally, and although there is some lateral convergence of the dorsoventrally more convex surface for the cuneiform with the concave surface for the fifth metacarpal, the lateral margins of these surfaces appear well separated. It should be noted, moreover, that proximomedially the unciform articulated with the magnum, somewhat as in *Meniscotherium*, but with relatively narrower contact, although Cope saw no facet for this on the unciform. Presumably that for the magnum blended too smoothly with the surface for the cuneiform in the specimen he examined. The facet is particularly evident on the magnum. As in *Meniscotherium* much of the dorsal portion of the medial surface articulates with the lunar and the dorsodistal part of this surface with the third metacarpal.

*Metacarpal I*.—The first metacarpal is somewhat reduced in *Meniscotherium*; about half the length of the third and with a relatively more slender and dorsally bowed shaft. The proximal extremity is noticeably enlarged with a convex articular surface for the trapezium which is elongated corresponding to the broad dimension of the trapezium's distal surface. I see no evidence for articulation with the second metacarpal. The distal extremity is enlarged but to a somewhat less extent with a transversely narrow and medially tapering articular surface for the first phalanx. The subdued keel appears displaced toward the lateral side.

The *Phenacodus* first metacarpal is evidently somewhat variable in length in comparison with the other metacarpals but appears

relatively more robust through the shaft than in *Meniscotherium* and is distinctly less bowed or arched. Proximally it evidently also articulated only with the trapezium.

*Metacarpal II.*—The second metacarpal of *Meniscotherium* is next to the third metacarpal in length and only slightly shorter. The greater part of the nearly triangular proximal surface articulates with the trapezoid. This facet is slightly convex dorsoventrally but distinctly concave transversely. Its lateral margin is a low ridge which divides the trapezoidal surface from a narrow somewhat distally deflected facet for the magnum. Distal to this on the lateral surface of the proximal extremity is a deep concavity with a somewhat distally facing dorsoventrally concave facet for the proximal extremity of the third metacarpal as the base of the second metacarpal overrides it. The medial side of the proximal extremity of the second metacarpal shows an arcuate facet along the proximodorsal margin for the trapezium. The shaft of the metacarpal is essentially straight and dorsoventrally somewhat flattened, but its width narrows only slightly from the base, then expands to the distal extremity which is a little wider transversely than the proximal portion.

The distal extremity shows an evenly rounded articular surface for the proximal phalanx, with a distinct keel only on the ventral half. The transverse axis of this convexity is slightly oblique to the long axis of the shaft.

The proximal extremity of the more robust *Phenacodus* second metacarpal is rather similar to that of *Meniscotherium*, although the trapezoidal facet is perhaps somewhat flatter and more nearly rectangular, and that for the trapezium of relatively smaller area. The shaft of the metacarpal, moreover, is not so slender and appears much less compressed dorsoventrally. The length of this bone in *Phenacodus primaevus* is at least two and one-half times that in *Meniscotherium chamense*, whereas the length of the humerus is a little less than twice that of the latter.

*Metacarpal III.*—Proximally the base of the third metacarpal in *Meniscotherium* has the form of a truncated triangle or trapezial outline, somewhat more so than that of the second metacarpal. The surface for the magnum is decidedly convex dorsoventrally but nearly straight transversely, sloping distally toward the medial margin and grading almost imperceptibly into a relatively broad marginal surface for the distally facing facet on the lateral side of the second metacarpal. The dorsal two-thirds of the lateral margin of the base of the third metacarpal exhibits a crescentic, nearly lateral facing

facet for the unciform, and distal to this, much as in the second metacarpal, there is a lateral concavity with a dorsoventrally concave, essentially distal facing facet accommodating a portion of the proximal surface of the fourth metacarpal, overriding it much as the second overrides the third. The shaft of the third metacarpal is much like that of the second but is a little longer and shows, moreover, a noticeable scarlike prominence on the medial side of the dorsal surface about a quarter of the length distally from the base, evidently for insertion of the extensor carpi radialis brevis. The distal articular surface for the proximal phalanx is similar to that of the second metacarpal but more nearly symmetrical, and the transverse axis is perpendicular to the long axis of the shaft.

The proximal extremity of the *Phenacodus* third metacarpal is much like that of *Meniscotherium* except that the surface for the second metacarpal is much more restricted and turns sharply distal with respect to that for the magnum. The lateral surface of the proximal extremity differs from that in *Meniscotherium* in that the facet for the fourth metacarpal is deflected somewhat more laterally. The shaft of the bone is relatively not so slender and is distinctly less compressed dorsoventrally.

*Metacarpal IV.*—The fourth metacarpal is appreciably shorter than the second, but because of the successively overlapping proximal extremities the distal extremities in the articulated foot are about even. The proximal surface of the *Meniscotherium* fourth metacarpal is more nearly triangular than on the second metacarpal. This surface is decidedly convex dorsoventrally but only slightly so transversely. Much of the triangular surface to the lateral margin articulates with the unciform and projects distally onto the lateral margin of the dorsal surface to a noticeable extent, corresponding to the extension of the dorsal lip of the unciform in its lateral part. Distal to the lateral margin of the proximal surface there is a concavity, not so deep as in the second and third metacarpals, and the facet for the fifth metacarpal is strongly arcuate, has a marked dorsal extension, but faces more laterally than in the second and third. The medial margin of the proximal surface is slightly offset distally in its dorsal portion for the overriding margin of the third metacarpal. The ventral portion of this surface, however, appears to be nearly separate, and is more oblique and may project proximally somewhat from the unciform facet. The shaft of the fourth metacarpal is relatively straight and dorsoventrally flattened as in the others. Its distal extremity shows a slight asymmetry in which the lateral half



of the articular surface has less diameter and its transverse axis is slightly oblique to the long axis of the shaft, the asymmetry being in reverse of that characterizing the second metacarpal.

In *Phenacodus* the proximal surface is relatively broader dorsally, and the lateral margin of surface for the unciform does not extend so noticeably distal on the dorsal surface. Moreover, the facet for the third metacarpal appears more sharply deflected from the unciform surface, and that for the fifth metacarpal faces more laterally than in *Meniscotherium*.

*Metacarpal V.*—The fifth metacarpal is approximately three-quarters the length of the fourth with a more slender and compressed shaft but with moderately large extremities. The dorsal surface of the bone is nearly straight so that the ventral surface appears distinctly concave longitudinally. This element in *Meniscotherium* is a little longer and distinctly more robust than the first metacarpal and is not so noticeably bowed. The proximal extremity is broad but not deep dorsoventrally. The surface for the unciform is strongly convex dorsoventrally, and transversely it is of nearly uniform width and straight or only slightly convex. Sharply deflected distally from the inner or medial margin of the unciform facet is an elongate, crescentic surface extending medially and distally for articulation with the fourth metacarpal. The distal extremity is a little smaller than that of the fourth but the form is nearly identical. Its asymmetry is not so striking as in the first metacarpal.

In the *Phenacodus* skeleton that Cope described, the fifth metacarpal is about the same length as the first but very much sturdier. In another articulated fore foot (A.M. No. 2961) the fifth metacarpal is much longer as well as heavier than the first. In either case the fifth is shorter relative to the fourth than in *Meniscotherium*. While short in comparison with *Meniscotherium*, the *Phenacodus* fifth metacarpal has a relatively much greater diameter. In an instance where the ratio of lengths is about two to one, diameters of the shaft are between three and four to one. The proximal extremity of the fifth metacarpal is deeper dorsoventrally in comparison with its width than in *Meniscotherium* and the facet for the fourth metacarpal is relatively smaller and does not extend distomedially so noticeably. Both exhibit a strong process or tuberosity on the lateral surface of the proximal extremity for the extensor carpi ulnaris.

*Phalanges.*—The proximal phalanges of the *Meniscotherium* manus are approximately half the length of the corresponding metacarpals. They are slender and of nearly uniform width, tapering only



slightly toward the distal extremity, that of the third digit being broadest. The proximal extremity of each is the deeper, corresponding to the distal extremity of the metacarpal, but through the shaft and distally they are rather flattened. The second phalanges in II to V are about two-thirds the length of the first in each, also slightly tapering and more flattened distally. The distal phalanges are about the length of the penultimate in each, with a slender shaft but distally spatulate. The dorsal surface is convex, and the ventral or palmar surface is flat. They have a surprisingly human appearance, and in all probability possessed a primatelike nail rather than hoofs or claws, as suggested by Marsh (1892, p. 448).

The *Phenacodus* phalanges are relatively shorter and much broader, and the broadly spatulate form of the distal or ungule phalanges in digits II to IV extends to the proximal extremity. The latter have been described as subungulate in character and are quite unlike those in *Meniscotherium*.

#### PELVIC GIRDLE

The innominate bone of *Meniscotherium* is moderately elongate with a strongly curved ilium flaring outward cranial to the auricular or sacral surface (see fig. 8). The ilium is essentially triangular in cross section from the acetabulum through most of its length, with the lateral (acetabular) border converging with, and then paralleling, the medial ventral (pubic) border toward the anterior superior spine at the ventrolateral extremity of the supra-iliac border. The external iliac or gluteal surface is strongly concave transversely in its mid portion, opposite the sacral surface, and the uniformly curved crest of the ilium commences caudad about opposite the posterior margin of the rugosity for the sacrum and swings forward and outward to the somewhat recurved anterior superior spine. This anterolateral extremity of the long crest of the ilium is distinctly rugged, possibly implying importance to the sartorius and tensor muscles, but surely significant for the superficial gluteus muscle which would be inserted on the third trochanter of the femur. The acetabular border has a curvature similar to that of the crest of the ilium and terminates caudad in a prominent and rugged anterior inferior spine extending forward from the margin of the acetabulum for the rectus femoris, a part of the extensor group for the shank.

The margin of the acetabulum is well separated by a broad dorsal surface from the ischial border and by a broad ventral surface from the pubic border. The cotyloid notch is deeply impressed and

directed posteriorly along the shaft of the ischium. The ischium is elongate, straight, and comparatively slender, with a transversely concave medial surface. The ischial spine is small but fairly acute; however, the ischial tuberosity is prominently developed, accommodating the biceps femoris and other flexors of the leg. The shaft of the pubis is somewhat flattened and slender. Unfortunately, the ramus of this bone and that of the ischium are poorly represented and badly preserved in the material at hand; nevertheless enough remains to indicate a large, oval-shaped obturator foramen.

The *Meniscotherium* innominate bone is surprisingly like that of *Phenacodus*, although the latter is relatively more elongate, and the crest of the ilium would appear to be more flaring and recurved. The ischial spine in *Phenacodus* is more rugged, but the ischial tuberosity may not be relatively so well developed. The anterior inferior spine of human anatomy seems prominent on the acetabular border of the ilium, but it may be noted that the "deeply impressed subtriangular fossa" described by Cope (1884b, p. 455) as located just above the position of the anterior inferior spine and near the edge of the acetabulum is much less significant in *Meniscotherium*.

The *Hyopsodus* innominate bone is elongate and slender. The ilium shows the similarly arcuate and flaring dorsal margin, but the gluteal surface may be a little less concave. The anterior extremity is missing in the specimen at hand. The base or posterior portion of the ilium is a little less trihedral in cross section with the pubic border on the ilium much more subdued than in *Meniscotherium*. There is little or no evidence for an ilio-pectineal eminence on the dorsal margin, although this is weak or subdued in *Meniscotherium*. The anterior inferior spine on the acetabular border, however, which supports the origin of the rectus femoris, is surprising well developed. The ischium is slender but possibly a little less elongate than in *Meniscotherium*. The ischial tuberosity is prominent and the ischial spine perhaps more so than in *Meniscotherium*. Much of the pubic bone is missing, as is the ramus of the ischium. The cotyloid notch in the acetabulum for the ligmentum teres is constricted but directed along the ischium much as in *Meniscotherium*.

#### FEMUR

The femur of *Meniscotherium* is comparatively robust, as noted by Cope in his very brief description, and its shaft is straight, although proximally the anteromedial margin is decidedly curved as it approaches the head (see pl. 8). The head may be somewhat oval

to nearly circular in proximal view and its neck moderately slender and anteromedially directed. The fossa for the ligamentum teres is noticeably posterior in position and essentially marginal, in keeping with the posteriorly directed cotyloid notch of the acetabulum. The greater trochanter is robust and extends proximally a little more than the head, from which it is separated by a well-defined notch. The posterior crest of the greater trochanter partially covers posteriorly a deep and elongate digital fossa into which are inserted the obturator muscles. Distally this comparatively thick or well-rounded crest appears to divide, and a more feeble, sometimes poorly defined crest or intertrochanteric line crosses the shaft distomedially to join the distal extremity of the medially outstanding, nearly triangular lesser trochanter for the iliopsoas on the posteromedial margin of the shaft. The apex of the lesser trochanter has a position about a quarter of the length of the bone distal to the proximal extremity. The better defined lateral portion of the posterior crest from the greater trochanter extends distally to join the prominent and flattened third trochanter, which is almost halfway down the shaft. The development of this process emphasizes, as in the horse, the importance of the superficial gluteus muscle in abducting the limb and flexing the hip joint. The outline of the third trochanter varies somewhat from a proximodistally elongate flare to a shorter but more laterally projecting prominence.

On the enlarged distal extremity the patellar trochlea is narrow, elongate, and prominently raised. The condyles are large and separated by a broadly open intercondyloid notch, and the lateral and medial surfaces of the extremity are strongly divergent posteriorly. The condylar tuberosities or epicondyles are noticeable, and the outer, more subdued, is at the extremity of the prominent lateral supracondyloid crest which extends distally from the third trochanter. A similar medial supracondyloid crest disappears a short distance proximally on the shaft.

Much that Cope said (1884b, pp. 455-456) about the *Phenacodus* femur applies to that of *Meniscotherium*, particularly with regard to the proximal extremity and much of the shaft, but I note that the greater tuberosity in *Phenacodus*, although anteroposteriorly deeper, is a little less extended proximally, and the shaft is relatively more robust. Distally the fossae at the posterior base of the condyles are much less significant in *Meniscotherium*, and the transversely oriented posterior portion of the inner articular surface is as wide as or wider, rather than narrower, than the more oblique or transversely



more convex outer articular surface in *Meniscotherium*. The patellar trochlea in *Phenacodus* seems broad, and the patella itself is comparatively wide and not so elongate and distally tapering as in *Meniscotherium* (see pl. 8).

The straight or but slightly curved *Hyopsodus* femur is slender, elongate, and somewhat flattened anteroposteriorly. The proximal extremity is transversely narrow, as the head and slender neck do not extend medially so noticeably as in *Meniscotherium*. The head, moreover, is nearly spherical and the fossa for the ligmentum teres is centrally located, well removed from the margin of the articular surface. The greater tuberosity is comparatively small and does not project proximally as far as the head. The digital fossa is proximodistally much shorter than in *Meniscotherium*, and the lesser tuberosity is nearer the proximal extremity. The lateral margin of the shaft from the greater tuberosity to the lateral condyle is compressed, and just beyond to the midpoint of the shaft is laterally expanded into a well-defined, proximodistally elongate third trochanter, with a rugged crest for the superficial gluteus muscle. The distal extremity of the *Hyopsodus* femur at hand is poorly preserved, but I note that the patellar trochlea is relatively broader than in *Meniscotherium*.

#### TIBIA

The *Meniscotherium* tibia is a little shorter than the humerus. It is relatively slender and noticeably bowed anteriorly (see pl. 9). It exhibits an elongate cnemial crest that is laterally deflected and extends straight nearly half the length of the shaft. The crest is distally somewhat roughened, evidently for the tendon of the semitendinous muscle which would have its origin at the prominent ischial tuberosity. From this point the crest rapidly subsides as a well-rounded ridge or margin crossing obliquely to the medial side and then directed more or less subdued toward the inner malleolus. Proximally the shaft shows a broad, gently convex anteromedial surface and narrower, concave lateral and posterior surfaces which are separated by a sharp posteromedial crest that would support the interosseous membrane. This crest curves strongly outward proximally to where it reaches the facet for the head of the fibula and distally swings somewhat forward and subdued to a more medial position at the place of contact for the distal extremity of the fibula. The posteromedial margin of the shaft is also acute proximally, beneath the medial tuberosity or condyle of the tibia but loses this



character distally, near the midpoint of the shaft. Distally, the shaft is slender and essentially rounded.

The proximal extremity of the tibia is broad and laterally overhanging. The two surfaces for the femur appear roughly equal. The medial surface is somewhat concave transversely but distally offset and broad posteriorly. Along the posterolateral margin of this there is a noticeable facet, offset or obliquely turned from the foregoing and adjacent to the popliteal notch, for attachment of the posterior crucial ligament. The outer surface for the femur rides smoothly up the median spine which forms the medial apex of the surface and accords with the transversely more oblique appearance of the outer articular condyle of the femur. The distal surface of the laterally overhanging outer condyle shows a small, convex, oval and almost distally facing facet for the fibula. On the anterior portion of the proximal extremity there is a distinct transverse notch or step which tends to define the proximal extremity of the cnemial crest and is evidently the position for attachment of the patellar ligament.

The distal extremity of the tibia is somewhat enlarged and exhibits a pronounced distal extension medially of the internal malleolus which articulates with the inner side of the astragalus. The distal articular surface shows a shallow, anteroposteriorly elongate concavity adjacent to the inner malleolus for the inner crest of the astragalus. The transversely more elongate outer surface for the medial side of the outer crest of the astragalus is decidedly oblique to the longitudinal axis of the shaft. This oblique facet terminates proximolaterally adjacent to the fibular contact.

Cope (1884b, pp. 503-504) has called attention to several differences between the tibia of *Meniscotherium* and that of *Phenacodus*. In the character of the cnemial crest, he noted that it is relatively shorter and more obliquely truncated proximally, and its distal extension does not cross to the internal malleolus in *Phenacodus*. With regard to "the early disappearance of the external posterior angle and its reappearance on the distal two-fifths of the length of the shaft" in *Meniscotherium*, I suspect that his specimen was unusual or defectively preserved, as seems evident in his illustration (1884b, pl. 25g, figs. 16, a, b, and c). His fifth point evidently refers to the disappearance on the middle of the shaft of the posterior inner angle, rather than the posterior external angle, because as actually stated this was part of his fourth point. He further noted that the posterior face of the shaft distally is roughened for muscular insertion in

*Meniscotherium*, and that the internal malleolus is obliquely truncate and acuminate as in many creodonts. In *Phenacodus* the internal malleolus is much more blunt. It may be further noted that the tibia in *Phenacodus* is essentially straight, not bowed as in *Meniscotherium*, and the shaft is much more robust.

A distal portion of a tibia is known for *Hyopsodus paulus*, as well as for *H. walcottianus*. Both show the anteroposteriorly concave surface for the astragalus which lacks any clearly defined median flexure, denoting a very shallow trochlear groove in the latter. This surface, moreover, is not so oblique transversely as in *Meniscotherium*. The internal malleolus is abruptly truncated distally and the rounded anteromedial margin becomes more anterior in position proximally on the shaft, in the direction of the cnemial crest. A lateral crest for the interosseous membrane is somewhat better defined in the *H. paulus* specimen, but at its distal extremity, at the margin of the astragalar facet, the internal malleolus is roughly acuminate and I find no evidence of a facet for the fibula.

#### FIBULA

The *Meniscotherium* fibula is a decidedly slender bone with moderately enlarged extremities (see pl. 9). The shaft is slightly thicker distally and this portion shows a better defined anteromedial crest for the interosseous membrane. The proximal extremity exhibits a proximally facing, anteroposteriorly elongate oval concavity for articulation with the external tuberosity of the tibia. The anteroposteriorly expanded proximal extremity affords attachment for muscles believed to be the peroneus longus and the soleus, and more medially the tibialis posterior, that aid in flexing and extending the foot. The distal extremity exhibits an oblique, distomedially facing surface which articulates with the outer side of the astragalus and with the calcaneum. On the lateral surface of the extremity is a short but prominent longitudinal crest or process bounding anteriorly a smooth, broad groove, evidently for the tendons of the peroneus muscles.

The *Phenacodus* fibula has a similar appearing proximal extremity, but the shaft is sturdier and the distal extremity more enlarged. It also appears that the fibula in *Phenacodus* makes a more expansive contact with the tibia, both proximally and distally. Moreover, the lateral crest or process on the distal extremity is much less developed than in *Meniscotherium*.

The distal portion of a fibula belonging to *Hyopsodus paulus* shows a somewhat enlarged external malleolus with an oblique facet

for the astragalus. The lateral margin of the distal surface is turned outward, evidently for some articulation with the calcaneum, but this marginal facet is anteroposteriorly convex rather than concave as in *Meniscotherium*. The lateral tubercle of the malleolus that bounds the groove for the peroneus longus anteriorly is somewhat more posterior in position, and the peroneal groove though narrower is well defined. The posterior margin of the preserved portion of the fibula is rather more sharply ridged than in *Meniscotherium*. Medially, the external malleolus is slightly roughened proximal to the astragalar facet, and there is no evidence of a facet for the tibia.

#### PES

The hindfoot of *Meniscotherium* (see pl. 10) appears to be as much as 25 percent larger than the forefoot, as determined by the length of the metatarsals relative to that of the metacarpals. The tarsus, however, does not appear to be so proximodistally compressed as the carpus, so that in dorsal aspect the tarsus more nearly resembles that of *Phenacodus*. Most noticeable differences from the *Phenacodus* foot lie in the appearance of the tibial surface of the astragalus and the shorter, more wedge-shaped cuboid in *Meniscotherium*. Moreover, the distal extremities of the metatarsals are relatively not so broad as in *Phenacodus primaevus*. The *Meniscotherium* hindfoot bears a resemblance also to the *Tetraclaenodon* hindfoot, but in the latter the elements are relatively more elongate and slender.

*Astragalus*.—The astragalus is a distinctive bone in *Meniscotherium*, somewhat compressed dorsoventrally on the medial side but not on the lateral side. The inner crest of the trochlea or tibial surface is subdued and rounded, whereas the lateral crest is high and acute. The neck is sturdy but elongate and directed medially as well as distally. The transversely broad head has a strongly biconvex navicular surface that tapers somewhat medially. The ventral surface of the astragalus, or that facing the calcaneum, exhibits two obliquely elongate and nearly parallel facets. The lateral or ectal facet is uniformly concave in its long direction and extends out on a prominent distolateral process. This process also deflects laterally the distoventral margin of the large, otherwise nearly vertical facet for the fibula. The medial or sustentacular facet is longitudinally convex and broader distally where it extends onto the neck. Posteriorly (proximally) this facet narrows and near its extremity is sharply flexed ventrally where it articulates with the acute posterodorsal margin of the sustentaculum. Lateral to this flexure and at



the posterior extremity of the deep groove for the interosseous ligament, separating the ectal and sustentacular facets for most of their length, is the ventral opening of the astragalar foramen. Dorsally this foramen opens near the posterior margin of the tibial surface. Between these apertures the posterior margin of the astragalus shows a smooth, very broad, shallow, and somewhat oblique groove interpreted as conducting the flexor longus hallucis. The medial surface of the astragalus, as noted by Cope (1884b, p. 505) "is oblique, and has a central fossa and a prominent shelf-like angle below it." There is apparently no articulation with the cuboid.

The *Phenacodus* astragalus is noticeably different in exhibiting a much better developed inner crest on the astragalus with a deeper trochlear groove which extends to the posterior margin. The medial or inner surface is essentially vertical, not nearly so oblique as in *Meniscotherium*. The neck of the astragalus is shorter, and with the head is relatively wider transversely than in *Meniscotherium*.

The *Hyopsodus* astragalus appears anteroposteriorly short, but the most noticeable feature in comparison with *Meniscotherium* is the much less raised outer crest of the tibial surface. The low, broadly rounded inner crest and the ventral shelflike inner projection are much alike in the two forms, but between the subdued inner and outer crests there is left only a very weakly developed trochlear groove. This also leaves the tibial surface transversely much less oblique than in *Meniscotherium*. The neck is somewhat oblique, nearly as in *Meniscotherium*, but appears relatively shorter. Matthew (1915) has described an astragalar facet on the cuboid; such an articulation, however, is not evident on the head of the astragalus at hand. The facet for the fibula is at a 90-degree angle from the tibial facet, less acute than in *Meniscotherium*. The lateral prominence of the anteroventral portion of the fibular surface, which supports anterior extension of the ectal facet beneath, is less projecting than in *Meniscotherium*. The oblique ectal and sustentacular facets on the ventral surface of the *Hyopsodus* astragalus are much like those in *Meniscotherium* but a little less elongate. The groove between them for the interosseous ligament is deeply impressed as in *Meniscotherium*, but the astragalar foramen in ventral view is more posteriorly placed. The groove on the posterior margin of the astragalus for the flexor longus hallucis is similarly broad and well defined, but dorsoventrally perhaps a little more elongate.

In the hindfoot of *Tetraclaenodon* the astragalus has an elongate neck and a relatively large head that is highly convex transversely.



The trochlea for the tibia is shallow but the inner crest, particularly posteriorward, is not nearly so subdued. The inner and outer walls of the astragalus are both somewhat oblique, lacking the striking difference noted in *Meniscotherium*. On the ventral surface the ectal facet is a short, oval concavity whose long axis is nearly transverse, more oblique to the sustentacular facet than in *Meniscotherium*. Moreover, it is interesting to note that the groove for the flexor longus hallucis on the posterior margin is surprisingly prominent, better defined than in *Meniscotherium*, and the astragalar foramen is not centrally located in the groove of the trochlea, but close to the inner crest.

*Calcaneum*.—The calcaneum of *Meniscotherium* is elongate with the posterior (proximal) projection comprising a little more than half the length. The bone is dorsoventrally deep and transversely somewhat compressed in the posterior half. It terminates posteriorly in an enlarged, slightly bilobate extremity for the Achilles tendon, extending posteriorly a little more on the medial than on the lateral side. A little forward of the middle of the calcaneum the astragalar condyle, as noted by Cope, is placed diagonally across the superior or dorsal ridge, with its convex articular facet facing anteromedially and slightly dorsally. Anterolaterally the condyle thickens and the rounded dorsal margin articulates with the distal margin of the external malleolus. A prominent ridge on the calcaneum extends anterolaterally to the well-developed peroneal tubercle near the anterior (distal) extremity, which bounds dorsally the broad groove for the peroneus longus. The sustentaculum is a prominent knob medial to the astragalar condyle, with a dorsally facing, transversely elongate oval facet for the astragalus. This facet turns sharply ventral on the posterior margin of the sustentaculum, as has been noted for the sustentacular facet of the astragalus. The posteroventral surface of the sustentaculum is smooth and broadly grooved for continuation of the extensor longus hallucis. The anterior or distal extremity articulates with the cuboid in a dorsoventrally concave and transversely highly oblique facet that extends posteromedially almost to the anterior margin of the sustentaculum. The dorsal margin of this oblique concavity extends dorsomedially from near the peroneal tubercle toward the neck of the astragalus and is less oblique or nearly at right angles to the long direction of the shaft. The more ventral margin extends ventromedially to the inferior margin of the calcaneum.

The *Phenacodus* calcaneum is similar but with stronger, more mas-

sive construction. The sustentaculum is deep and thick, not so elongate and slender. The lateral crest from the astragalar condyle to the peroneal tubercle is rugged and outstanding, but with less definition of the tubercle itself. The surface for the cuboid extends ventromedially somewhat oblique, but is much less concave, evidently lacking the flexibility of the *Meniscotherium* articulation.

The *Hyopsodus* calcaneum is relatively shorter than that of *Meniscotherium*, and the posterior portion between the astragalar condyle and the enlarged tuberosity for the Achilles tendon is a little more compressed transversely. The astragalar condyle is similar but a little less dorsally projecting. The sustentaculum is dorsoventrally more compressed, but anteroposteriorly broader and perhaps a little less extended medially. The shortened anterior portion of the calcaneum, correlated with the relatively short neck of the astragalus, exhibits a somewhat less oblique and less concave facet for the cuboid, although in its transverse direction it is nearly aligned with the anterior margin of the sustentaculum. The dorsal margin of this surface is transversely shorter and more curved, with a long lateral margin extending down to a more ventrally placed peroneal tubercle. The peroneal groove consequently is decidedly more ventral in position.

The slender *Tetraclaenodon* calcaneum has a long anterior or distal portion, in keeping with the elongate neck of the astragalus, as well as a lengthy posterior portion. The sustentaculum is slender and outstanding, about as in *Meniscotherium*. The articular facet for the cuboid, although oblique and concave, is rather less so than in *Meniscotherium*, and it does not approach so near the sustentaculum posteromedially.

*Navicular*.—The *Meniscotherium* navicular is proximodistally short and has a deeply concave proximal surface occupied entirely by the head of the astragalus. The rim of the concavity is broadly curved dorsally and medially, but the lateral margin is more nearly straight and rises to a low prominence ventrolaterally. The medial margin, however, rises to a higher, more acute process ventrally, and between these there is a sharp notch in the ventral border for passage of the tendon of the posterior tibialis. The lateral side of the distal surface shows a flat facet for the external cuneiform which is dorsoventrally elongate and noticeably tapering ventrally. Medial to this the facet for the middle cuneiform is dorsoventrally shorter and distinctly convex. The more ventromedial surface of this convexity articulates with the internal cuneiform, and rises to the prominence

at the ventromedial angle of the proximal surface. The lateral surface of the navicular shows a dorsoventrally elongate and slightly convex facet along its more proximal portion for articulation with the cuboid. On the ventral surface of the navicular, lateral to the notch, is a small knob or process that may have supported a part of the insertion for the tibialis posterior. It is located just above the posterior extremity of the facet for the external cuneiform but in *Meniscotherium* evidently does not make contact with that bone.

A few differences were noted with respect to the *Phenacodus* navicular, although the two are rather similar. On the proximal rim the ventrolateral prominence is more significant than that of the ventromedial angle, and projects laterally as well as proximally in *Phenacodus*. The more obliquely facing facet for the cuboid is proximodistally deeper and rides well up on the proximoventral prominence. Also, the ventral tubercle is larger, more median in position, and its distal surface carries a small facet, not seen in *Meniscotherium*, for articulation with the ventral extension of the external cuneiform. The facet for the middle cuneiform appears relatively longer and less convex.

In the *Tetraclaenodon* navicular the ventral tubercle and the ventrolateral prominence of the proximal rim together form a strongly developed, oblique, and ventrolaterally projecting process. This results also in a dorsoventrally concave surface articulating with the cuboid.

*Cuboid*.—The *Meniscotherium* cuboid viewed dorsally in an articulated foot appears relatively short proximodistally, with the exposed area in the form of a parallelogram or nearly rectangular, inasmuch as the articular surface for the calcaneum extends distally well down the dorsal surface. Disarticulated, the calcaneal facet is seen to be dorsoventrally very convex and highly oblique in a nearly transverse plane. Moreover, the dorsal and ventral surfaces are convergent in a proximolateral direction. Distally the ventral surface shows a pronounced ventromedial flare, ventrally covering the deeply impressed peroneal groove. The distal surface anterior to the elongate peroneal groove is nearly oval in shape and essentially concave both dorsoventrally and transversely. The surface is principally for articulation with the fourth metatarsal, although the lateral extremity of the transversely elongate oval flattens out or is somewhat deflected proximally for articulation with the fifth metatarsal. Also, the ventral margin of the oval facet is rounded into the peroneal groove for the recurved surface of the fourth metatarsal. The proximal portion



of the broad medial surface of the cuboid has a dorsoventrally elongate facet for the navicular. On the distal portion of this surface the facet for the external cuneiform is variable and may be dorsoventrally long and possibly bilobate or separated into two parts. Occasionally the surfaces for the navicular and external cuneiform are in contact or partially merged.

The *Phenacodus* cuboid is much more elongate, and the proximal surface though convex and oblique is much less so than in *Meniscotherium*. The broad distal articular surface also provides a relatively larger area for the fifth metatarsal. The ventral surface is broadly expanded and ventrodistally flaring, extending well down over the peroneal groove but does not appear so triangular in outline as in *Meniscotherium*. On the medial surface the large facet for the navicular is proximovertrally located and about as deep as it is long.

In *Tetraclaenodon* the cuboid is decidedly slender and elongate in dorsal view, and the proximal extremity is more like that of *Phenacodus*. The ventral surface although expanded over the peroneal groove is relatively much narrower transversely, and the medial surface is narrower dorsoventrally. Also, the facet for the navicular is noticeably convex dorsoventrally. It is straight or slightly concave in *Meniscotherium*.

*Internal cuneiform.*—The internal cuneiform is flattened with its medial facing surface relatively broad and long. Proximally this surface in *Meniscotherium* narrows and its proximodorsal margin is deeply concave for articulation with the navicular. Marginal to this concavity the lateral surface exhibits an arcuate facet, convex in its more dorsal portion but concave proximally, that articulates with the medial side of the middle cuneiform. The distal extremity, which extends well beyond the middle cuneiform, has a dorsoventrally elongate concavity for articulation with the first metatarsal. There does not appear to be any definable facet for the second metatarsal in the material at hand.

The *Phenacodus* internal cuneiform is similar appearing, but the ventral margin is thicker, and the dorsoventrally elongate facet for the navicular is less concave and faces more nearly proximal. In consequence the relatively flattened facet for the middle cuneiform has a more dorsoventral orientation. Except for its thicker ventral margin the *Tetraclaenodon* internal cuneiform more nearly resembles that of *Meniscotherium*, notably in the deeply concave, proximodorsally placed navicular facet. The distal extremity is similar in all three forms.



*Middle cuneiform.*—The dorsoventrally elongate middle cuneiform is the smallest element of the *Meniscotherium* tarsus. Its limited dorsal surface has convex proximal and distal margins that lap slightly onto the dorsal surfaces of the navicular and second metatarsal respectively. Both the proximal and distal surfaces of the element are dorsoventrally concave, that for the navicular more decidedly so. The surface for the second metatarsal is, moreover, transversely convex and tapers ventrally. The medial and dorsoventrally compressed lateral surfaces of the middle cuneiform articulate in an uneven, arcuate facet with the internal cuneiform and in a narrow dorsoventrally elongate facet with the external cuneiform respectively. Behind the upturned ventral margin of the navicular surface a small but distinctly rugose prominence, and possibly the adjacent tip of the internal cuneiform, may well have received a part of the tibialis posterior, which extending through the ventral notch of the navicular would have been inserted as well on the ventral tubercle of that bone, as mentioned in a foregoing section. This muscle, of course, functions with the peroneus longus in extending the tarsus, and against it in turning the foot inward.

The *Phenacodus* middle cuneiform is much like that in *Meniscotherium*, but the proximal and distal facets, though similar, are a little more flattened, notably that for the navicular. This is true also for the *Tetraclaenodon* middle cuneiform, and the dorsal surface is more nearly square. The medial facet for the *Phenacodus* internal cuneiform is also relatively flat and essentially straight, rather than arcuate. It may be further noted that the ventral tubercle, evidently for the tibialis posterior, though large in *Phenacodus*, is relatively not so rugged as in *Meniscotherium*. This portion of the *Tetraenodon* middle cuneiform is missing in the specimen examined.

*External cuneiform.*—The external cuneiform is significantly larger than the middle cuneiform in *Meniscotherium*, with its surface for the third metatarsal more distal than the corresponding surface on the middle cuneiform. The dorsal surface on some specimens appears to be nearly twice as long proximodistally as that of the middle cuneiform. The proximal surface for the navicular is dorsoventrally elongate and ventrally tapering. That on the distal surface for the third metatarsal is also dorsoventrally elongate but somewhat projecting ventrally, and distinctly concave. It is also transversely broad anteriorly and markedly constricted about midway. The medial surface shows a narrow, dorsoventrally elongate facet, adjacent to the proximal surface, for articulation with the middle cuneiform. Distal to

this on the medial surface there are two well-separated, oval facets adjacent to the distal surface, for articulation with the second metatarsal. The lateral surface of the external cuneiform on its more proximal portion shows the dorsoventrally elongate, but variable and often bilobed, surface for the cuboid. On the proximal portion of the transversely narrow ventral surface there is an elongate process that extends somewhat medially as well as ventrally and exhibits a distally deflected, hooklike extremity. The concave portion bounded proximally by this hooklike process, and in part distally by the ventral extension of the distal surface, is the continuation medially of the peroneal groove, so well defined on the cuboid. The ventral process of the external cuneiform extends beyond that on the middle cuneiform, and while it may have included an insertion of the tibialis posterior, it no doubt supported part of the ligamentous cover of the peroneus groove and probably tendon for certain of the interosseous muscles.

The *Phenacodus* external cuneiform differs only in minor respects from that of *Meniscotherium*. The distal articular facet for the third metatarsal is less concave dorsoventrally. That laterally for the cuboid is generally large and oval shaped, not extending onto the ventral process. The ventral process appears to be relatively a little shorter but deeper and more massive.

The external cuneiform of *Tetraclaenodon* is proximodistally elongate and relatively more slender, dorsoventrally as well as transversely, than in *Meniscotherium*. The facet for the cuboid is rather like that in *Phenacodus*. The ventral process is missing on the specimen examined.

*Metatarsal I.*—The first metatarsal, the smallest of the five in *Meniscotherium* is about half the length of the second, and its slender dorsally bowed shaft is more compressed transversely than dorsoventrally. The extremities are somewhat enlarged, the proximal extremity being the larger, with a simple, dorsoventrally convex proximal surface for the internal cuneiform. This surface, moreover, is broad and slightly convex transversely as well, permitting abduction as well as flexure and extension. Ventrolaterally the base is roughened and may be enlarged, evidently for the terminal or most medial insertion of the peroneus longus. The distal articular surface is dorsoventrally convex and shows a weak median keel. It is, moreover, relatively narrower and more oblique than in the second metatarsal.

The *Phenacodus* first metatarsal has about the same relative length

as in *Meniscotherium* but is comparatively straight and not nearly so slender. The *Tetraclaenodon* first metatarsal, however, is relatively longer, being nearly two-thirds the length of the second, and only a little more slender. The shaft is somewhat bowed as in *Meniscotherium*. The base or proximal extremity, it is further noted, exhibits a short ventrolateral spur, unlike *Meniscotherium*, and the articular surface for the internal cuneiform is only slightly convex.

*Metatarsal II.*—The second metatarsal of *Meniscotherium* is intermediate in length between the third and fourth, but its distal extremity is about even with that of the fourth in the articulated foot, because of the more proximal position of the base of the second metatarsal. The proximal surface for the middle cuneiform is nearly triangular in outline, dorsoventrally elongate and slightly convex. Transversely the facet is distinctly concave. The medial surface of the base is somewhat roughened and a short distance distally exhibits a low knob. Apparently, however, there is no faceting for either the internal cuneiform or the first metatarsal. The lateral surface of the base, however, shows a slightly concave facet proximodorsally and a smaller flattened facet proximoventrally for the external cuneiform. More distally, the lateral surface conforms to the medial surface of the third metatarsal base, but I find no evidence of articular contact. The shaft maintains a width at least as great as the base, becoming little wider distally, and is relatively compressed dorsoventrally. It is essentially straight but may be slightly bowed dorsally in some individuals. The convexity of the transversely wider distal extremity is slightly oblique and shows a pronounced median keel only on the ventral surface.

Except for its more flattened proximal extremity for articulation with the middle cuneiform and relatively wider distal extremity, the second metatarsal in *Phenacodus* appears very much like that in *Meniscotherium*. That in *Tetraclaenodon* is more elongate and relatively slender. The proximal surface of the base, like that in *Phenacodus*, is flattened although the outline is similar to that in *Meniscotherium*. The distal extremity is broad in comparison with the width of the base, but these are small relative to the length of the shaft.

*Metatarsal III.*—The *Meniscotherium* third metatarsal averages about 5 or 6 percent longer than the second. The shaft is broad and flat, increasing somewhat in width distally. The proximal extremity shows the asymmetric T-shaped base so frequently encountered in the mammalian third metatarsals. This surface for the external cunei-



form is gently convex dorsoventrally, slightly oblique transversely, and markedly constricted ventral to the broad and dorsally convex superior margin. The constriction is greatest on the lateral side, and ventral to this the ventrolateral margin of the surface for the middle cuneiform may be slightly deflected proximally. Adjacent to this there is a small flattened facet on the lateral surface for the ventral portion of the fourth metatarsal base. Dorsal to this facet on the lateral side of the third metatarsal there is a deeply concave, ventrolaterally facing surface for articulation with a medial knob or prominence close to the proximal extremity of the fourth metatarsal. The medial surface of the base of the third metatarsal shows a distinct knob, proximodorsally, that fits into a depression distal to the dorsal facet for the external cuneiform on the base of the second metatarsal. The convexity of the relatively broad distal extremity has an axis at right angles to that of the shaft and exhibits a prominent keel ventrally.

The similar appearing *Phenacodus* third metatarsal, as the second, has a generally flatter proximal surface for the external cuneiform and a relatively broader distal extremity. It should be noted, however, that the proportions of the metatarsals as outlined here apply more particularly to comparison with *Phenacodus primaevus* material, as the *Phenacodus copei* metatarsals are relatively elongate and slender, somewhat more as described for *Tetraclaenodon*.

*Metatarsal IV.*—The *Meniscotherium* fourth metatarsal is a trifle shorter than the second, and somewhat more so than the third, as noted above. The shaft is dorsoventrally compressed but more slender than that of the third and has a slight lateral curvature so that the distal extremities tend to diverge. The proximal surface for the cuboid is dorsoventrally and transversely convex over its broader dorsal portion, but the narrower, ventromedially directed part is noticeably deflected proximally, so that the ventral margin of the base extends into the deeply impressed peroneal groove of the cuboid. Adjacent to the recurved ventral portion of the cuboid surface, on the medial side of the fourth metatarsal, is a facet for the third metatarsal. A prominent knob on the medial side of the base, just distal to the dorsomedial margin of the cuboid facet, is convexly faceted for the concavity on the lateral side of the third metatarsal base. The lateral side of the fourth metatarsal base is also deeply concave and exhibits a distolaterally and somewhat ventrally facing concave facet for the fifth metatarsal. The convexity on the distal



extremity of the fourth metatarsal is narrower laterally and its axis is slightly oblique, more distal on the medial side.

Differences from the *Phenacodus* and *Tetraclaenodon* fourth metatarsal are essentially those noted with regard to the second and third metatarsals, but it may be noted that the ventral portion of the cuboid facet is not nearly so recurved, so that in these forms the base of the fourth metatarsal does not extend so noticeably into the peroneal groove.

*Metatarsal V.*—The fifth metatarsal of *Meniscotherium* is a little longer than the first and about two-thirds the length of the fourth. The shaft is compressed in a dorsolateral-ventromedial direction, and the broadly expanded proximal extremity is gently deflected ventromedially. The base is essentially trilobed with a dorsomedial lobe or prominence that articulates with the lateral concavity in the base of the fourth metatarsal. The margin from this lobe to the more proximoventral lobe lies adjacent to the lateral margin of the cuboid surface of the fourth metatarsal. With the posterior margin of this latter surface, the proximoventral lobe of the fifth metatarsal extends into the peroneal groove and, I suspect, receives a portion of the insertion of the peroneus longus. The third or ventrolateral lobe probably includes insertion of the peroneus brevis, an extensor from a more dorsal direction.

The *Phenacodus* fifth metatarsal is also about two-thirds the length of the fourth, but is straighter and much more robust. Its proximal extremity lacks the trilobed appearance, and the articulation with the cuboid is not so oblique to the shaft. The base of the fifth metatarsal in *Tetraclaenodon* is transversely flattened, somewhat as in *Meniscotherium*, and exhibits a prominent ventral knob, evidently for the peroneus longus, which is less proximally directed than in *Meniscotherium*, but the ventrolateral process, noted in the latter, is missing.

*Phalanges.*—The proximal phalanges in the second to the fourth digits are a little less than half the length of the metatarsals. They are broad but taper somewhat distally and are flattened, particularly the shaft, and the distal extremity is much more compressed dorso-ventrally than the proximal. The second phalanges are nearly two-thirds the length of the first in each digit and are also distally tapering and flattened. The phalanges of the third digit are broader than those of the second and fourth. The distal phalanges are elongate but a little shorter than the first, with a somewhat spatulate anterior half and a narrow posterior neck. The spatulate portion is dorsally

convex and ventrally flat, and there is a small dorsal depression near the anterior margin which itself is not notched or fissured.

The *Phenacodus primaevus* phalanges are relatively shorter and broader, and the distal phalanges are more broadly spatulate with little or no posterior neck. The *Tetraclaenodon* phalanges are long and slender, not flattened, and the distal phalanx in each digit is transversely compressed and very little spatulate, clearly for a more clawlike structure. Matthew (1915) described the *Hyopsodus* phalanges as short, with the unguals clawlike, fissured, and not compressed.

### SUMMARY OF RELATIONSHIPS

Although the highly selenodont teeth of *Meniscotherium* early gave rise to considerable speculation as to its relationships, particularly to such perissodactyls as the chalicotheres and propalaeotheres, to the hyracoids and to the notoungulates, there is no doubt of its condylarthran affinities. While it differs importantly in many characters, evidently of more adaptive significance, from the typical condylarth *Phenacodus*, its rather numerous resemblances, presumably of conservative or basic significance, demonstrate a closer affinity to *Phenacodus* than to any other mammal whose skeleton is adequately known. This relationship, nevertheless, is best expressed by their being retained in separate families of the order. Similarities were also noted in comparisons with the limited skeletal materials of *Hyopsodus* available, but while rather striking in certain instances, the degree of relationship is perhaps a little less close than with *Phenacodus*.

*Meniscotherium* would appear to be rather less like *Tetraclaenodon*, although the latter is generally regarded as being in an ancestral position with regard to *Phenacodus*, and it was largely on the basis of this relationship that Matthew (1897) concluded that the more serially arranged foot structure characterizing *Phenacodus* was not primitive but secondary. The somewhat less fully acquired serial arrangement in *Meniscotherium* than in *Phenacodus* must then have been a parallel development, if not truly primitive, as I would not postulate *Tetraclaenodon* in an ancestral position to *Meniscotherium*.

Structural resemblances to the predaceous arctocyonids, with which the condylarths no doubt converged in much earlier time, show certain rather generalized similarities, but the interlocking elements in both the carpus and tarsus and the more significant differences in the astragalus and calcaneum suggest that the relationship to *Menisco-*

*therium*, clearly the most distinctly herbivorous of the condylarths, is rather remote. Nevertheless, this relationship is evidently less remote than that to the periptychids on the basis of teeth as well as feet, although the latter are now usually included within the Condylarthra. The periptychid foot structure as represented by *Ectoconus* is not condylarthran but of the taligrade type, as observed by Matthew, more closely allied to that of the pantodonts. A foot structure of this type was also observed for the tillodonts, whose teeth incidentally are basically more *Pantolambda*-like than arctocyonic. A slight resemblance between lower molars of *Meniscotherium* and *Esthonyx* deserves comment, although the two patterns are truly different and any thought of relationship is discredited by the upper molar structure as well as feet.

A relationship to the perissodactyls was early predicated on tooth structure as outlined in a foregoing section, but this was abandoned as more became known of the foot structure in *Meniscotherium*. The tooth structure somewhat less closely resembles that of the chalicotheres than perhaps certain of the Old World palaeotheres, although discrepancies in detail may be observed such as the somewhat more crescentic character of the protoconule in the upper molars and the very different third lower molar in *Meniscotherium*. Resemblances in molar structure are no doubt due to parallelism in development of the selenodont or crescentic tooth pattern, inasmuch as the interlocking arrangement of the elements of the carpus in the early perissodactyls readily excludes *Meniscotherium* from a close relationship.

The artiodactyls are even more remote, and although a roughly similar selenodonty has occurred in certain forms, as far as I can determine, the structures are not all homologous. Generally the position of the hypocone has been taken by the metaconule in early development of the selenodont pattern in upper molars of artiodactyls (or by the protocone in the cainotheres), but these would both appear to be definable in *Meniscotherium*. The artiodactyl foot structure, of course, is quite unlike that in *Meniscotherium*.

A resemblance which may be more than casual involves the late Paleocene and early Eocene litopterns of South America. The relative age of the São José de Itaboraí, as well as the Casamayor assemblage, however, would seem to preclude the possibility of *Meniscotherium* having given rise to these earlier proterotheriids, as would be implied in Wortman's postulation. Ameghino was, no doubt, closer to the truth in suggesting a common but as yet undiscovered ancestry. Perhaps the closest resemblance is seen in a comparison



with the proterotheriid *Anisolambda* which de Paula Couto (1952) has shown includes *Josepholeidya*, and occurs in beds regarded as of late Paleocene age in Brazil. Remarkably selenodont for so early a form, nevertheless I note a somewhat different trend in the development of the accessory cuspsules of the upper molars. The protoconule, for example, is less crescentic and more closely connected to the protocone, whereas the metaconule may be somewhat crescentic but shows little or no tendency to form a metaloph with the hypocone. The lower molars are perhaps less easily distinguished from those in *Meniscotherium* and show the metastylid crest as in the latter, but I note that the trigonid is relatively a little shorter anteroposteriorly and the labial wall of the protoconid perhaps more acute.

The litopterns are presumably of condylarthran affinity, as well as the more bunodont didolodonts which are included within the latter order, so that *Meniscotherium* may not be too distantly related to such a form as *Anisolambda*; nevertheless, one was not derived from the other as presently defined, and there is no evidence to show that *Meniscotherium* represents a return to the Northern Hemisphere of a South American condylarth.

The possibility of a close relationship between *Meniscotherium* and the hyracoids provoked considerable speculation during the earlier history of investigation. I am inclined to believe, however, that the relationship is decidedly remote. I suspect that much of the resemblance between them is adaptive in nature. There would appear to be certain similarities in form and proportions but the details often seem incompatible with any close affinity. There is, of course, a great interval of time between the recent hyracoids and *Meniscotherium*, as well as a wide geographic separation, and certain of the more obvious differences in the skull may be attributed to its shortening and the increase in the relative size of the brain.

The shortening of the skull has resulted in the orbits being farther forward with respect to the molar teeth, greatly affecting the orbital plate of the maxilla, and with the convergence anteriorly of the orbital margin of the frontals the possibility of binocular vision is much better in the hyracoids than in the meniscotheres. Moreover, the orbit is almost closed posteriorly by processes from the jugal and parietal. The postorbital processes of the frontals only are well developed in *Meniscotherium*. The parietals are not involved. Another feature of interest in skull shortening is the more vertically elongate and backward-facing pterygoid fossae, nearly as in man.



The glenoid surface for articulation with the lower jaw also has a nearly human appearance in its sigmoid flexure, quite unlike *Meniscotherium*. It should be particularly noted that the jugal participates in the glenoid articular surface and extends backward above this, almost completely obscuring the zygomatic process of the squamosal in lateral view. There would appear to be no tendency toward reduction of the zygomatic process of the squamosal in *Meniscotherium*. Anteriorly, however, the jugal is not so extended and does not reach the lachrymal, as it does in *Meniscotherium*, so that the maxillary forms a part of the orbital rim.

With the more expanded brain case there is much less development of the temporal or sagittal and lambdoidal crests, and the mastoid has a distinct lateral as well as occipital exposure. This bone, however, is even more nearly excluded from the basicranial surface than in *Meniscotherium* and is exposed only on the anterolateral margin of the root of the paroccipital process, posterior to the external auditory meatus. The hyracoid skull also retains a clearly defined interparietal in fully mature specimens. This has never been found in *Meniscotherium* or observed in any of the other condylarths for which skull material is known.

The cheek teeth of the modern hyracoids are specialized somewhat similarly to those in *Meniscotherium*, but the upper are more lophodont and a little less crescentic. Moreover, the premolars have become so completely molariform that few clues are left as to the stages through which the pattern may have developed. Also, incisor specialization has become highly distinctive. A more interesting comparison may be made with the early Oligocene forms of Africa, such as *Megalohyrax* and *Saghatherium*. While molarization of the premolars is well advanced, as in the later forms, the upper molars are rather more crescentic, particularly in the outer walls. A most noticeable difference from *Meniscotherium* is the weak or obscure character of the accessory cuspules in the upper series, particularly the protoconule which is so well developed and crescentic in *Meniscotherium*. In this respect the early hyracoids more nearly resemble the Cernaysian *Pleuraspidotherium*, at least as far as the molars are concerned.

The number of presacral vertebrae in hyracoids is the greatest for any of the living land mammals, and while *Meniscotherium* has one more lumbar vertebra than *Procavia*, I suspect that the number of dorsals was much less, as inferred from *Phenacodus*. The scapula has a very different appearing spine, proximally subdued and entirely

lacking the acromion and metacromion, so well developed in *Meniscotherium*. In the pelvic girdle the ilium is relatively very long and straight, quite unlike that in *Phenacodus* or *Meniscotherium*.

In the forelimb of *Procavia* the proximal extremity of the humerus is similar to that in *Meniscotherium*, but the distal trochlea shows a more simple, grooved pulley construction and there is no entepicondylar foramen. The distal articular surface of the ulna for the cuneiform is highly concave rather than convex as in *Meniscotherium*, and that of the radius for the scaphoid and lunar is distally extended on the scaphoid side, binding the carpus medially, much as the peculiar extension of the medial side of the tibia effectively binds the astragalus medially. Individually the elements of the carpus bear almost no resemblance in detail to those of the Eocene condylarth, although there is some approximation to the serial alignment. The recent hyracoid carpus, moreover, retains a separate central, and the first digit is reduced to a vestige.

Differences in the hind limb are noted in the very proximal position of the third trochanter and the very broad patellar trochlea on the femur and the tendency toward coossification of the tibia and fibula, as well as of the radius and ulna in the fore limb. The tarsus is noticeably different in the peculiar offset of the neck and head of the astragalus, and the articulation between the astragalus and calcaneum is principally through the enlarged ectal facet, there being no sustentaculum on the calcaneum. Moreover, the articulation between the calcaneum and cuboid is nearly flat, as is that between the astragalus and navicular.

*Pleuraspidothierium* from the Paleocene at Cernay, France, would appear to be condylarthran and possibly related to *Meniscotherium*. Moreover, there seems to be logic in including them in the same family, although some of the differences are rather striking, so that I cannot believe that *Meniscotherium* was derived from this form. Possibly P<sup>3</sup>-M<sup>3</sup> in *Meniscotherium* could have evolved from teeth of the form seen in *Pleuraspidothierium*, but the long diastema ahead of these teeth in the latter, the reduction in size and single-rooted character of the anterior upper premolars, as well as the frequent reduction in number of the lower series (see D. E. Russell, 1964), would surely preclude it as an ancestor.

The problem of relationship may be further complicated by a question of homology, relating to certain upper molar cusps. Simpson (1929) in discussing *Pleuraspidothierium* and *Othaspidothierium* in relation to *Meniscotherium* refers to the posterointernal cusp as a

"pseudhypocone" or displaced metaconule. This would imply a cusp origin similar to that of the early selenodont artiodactyls, and the upper molars do show a surprising resemblance to some of the selenodont forms of the later American Eocene. Support of the metaconule origin for the posterointernal cusp might be inferred from the development, although weak, of the cingulum around the "pseudhypocone" in *Pseudaspidotherium*. The hypocone from an origin on the cingulum would less likely show this, unless a secondary cingulum were developed. The evidence from *Meniscotherium* would appear to contradict such an origin for the posterointernal cusp, as this cusp seems to have originated from the cingulum, from the evidence of the premolars, for what it is worth, as well as from the cingulum itself. P<sup>3</sup> and P<sup>4</sup> of *Meniscotherium* suggest between them something of the transition in the relations of the generally well defined accessory cusps to the deutocone and tetartocone. Moreover, the posterointernal cusp of the molars, as well as the tetartocone of the premolars, seems to be an integral part of the cingulum. The latter shows no tendency to divide as in *Pleuraspidothierium*. The posterior upper premolars are rather *Phenacodus*-like, as observed by D. E. Russell (1964), so that the relations there of the metaconule and tetartocone are missing. I am much inclined to consider that the *Meniscotherium* upper molars, though decidedly selenodont, have a cusp pattern essentially homologous with that in the *Tetraclaenodon-Phenacodus* line, with the posterointernal cusp as the hypocone. If it can be demonstrated that the cusp in this position is not homologous in *Pleuraspidothierium* (and *Orthaspidothierium*) the meniscotheriid relationship certainly becomes much weakened.

Russell (1964) has given a detailed description of the skull of *Pleuraspidothierium*, and Pearson (1927), as well as Russell, has presented the characters of the basicranium. In a comparison of the basicranium of *Pleuraspidothierium* with that of *Meniscotherium*, however, a number of features are noteworthy. The pterygoid fossa is well developed, and although the walls are broken down they are not so flaring, and it would appear that the fossa is not carried so low with respect to the basisphenoid or the roof of the narial passage as in *Meniscotherium*. Posterior to this fossa there is no evidence for an alisphenoid canal in the position that it is found in *Meniscotherium*. The foramen ovale is prominently displayed in about the same position relative to the foramen lacerum medium, but less widely removed from the glenoid surface. The glenoid surface, though not complete in the specimen examined, does not appear to be so elongate antero-



posteriorly or so concave transversely. The postglenoid process may be more rugged and posteriorly better envelops the postglenoid foramen. The crest posterior to the foramen ovale, though damaged, seems prominently developed but possibly not so compressed transversely as in *Meniscotherium*. Posterior to the position of the external auditory meatus the mastoid process, which carries a lamina of the squamosal on its anterior face, is much more elongate in an anteromedial-posterolateral direction. Also, the extent of the mastoid exposed ventrally between the mastoid and paroccipital processes is much greater than in *Meniscotherium* in the skull that I examined. This, however, is evidently not constant, as Russell, in pointing out the variability of the paroccipital process, has indicated that it is sometimes indistinct and then closely applied to the mastoid process. According to Pearson (1927) the greater part of the paroccipital process is formed of the mastoid. It is apparently never developed as in *Meniscotherium*.

The petrous portion of the periotic in *Pleuraspidotherium* is very differently shaped than in *Meniscotherium*, as it is broad posteriorly and very rapidly tapering anteriorly. The slenderness of the anterior portion is suggestive of *Hyopsodus*, although in the latter it is not as broad posteriorly and more smoothly conical. The sulcus facialis would seem rather similar in the two forms, and the aperture for the facial nerve appears similarly situated, although the positions of the fenestrae ovalis and rotunda cannot be precisely determined because of damage to the specimen examined. Posteriorly the facial sulcus is directed downward toward the position of a stylomastoid foramen opposite the posterior extremity of the exposed petrosal, but this is farther back with respect to the medial root or extremity of the mastoid process than in *Meniscotherium*. Lateral to the facial sulcus there is much more of an epitympanic recess in *Pleuraspidotherium*. In *Meniscotherium* the mastoid portion lateral to the sulcus is essentially flush with the medial margin of the squamosal above the external auditory meatus, although separated from it by a groove.

Medial to the petrosal the lateral portion of the basioccipital is deep and broadly grooved, which forward leads to the foramen lacerum medium. Presumably this was occupied by the internal carotid, as suspected for a rather similar appearing structure in *Meniscotherium*.

The limb and foot material attributed to *Pleuraspidotherium* seem rather condylarthran, certainly not artiodactyl in form, but, as cautioned by Pearson (1927), these were not found in direct associa-



tion with teeth so that their allocation is speculative and based on relative abundance. These elements were figured and briefly described by Teilhard de Chardin (1921-1922), and certain of them were compared by Simpson (1929) to *Meniscotherium*. The distal part of the humerus figured by Teilhard de Chardin resembles that of *Meniscotherium* although the crests of the trochlea are less pronounced and there is evidently no entepicondylar foramen as Simpson noted. The proximal position of the lesser and third trochanter and the shortness of the digital fossa of the femur are rather unlike *Meniscotherium*, and I note in this a greater similarity to the recent hyracoids. The distal extremity of the femur is also rather dissimilar in the relatively smaller condyles. The shorter and wider patellar groove noted by Simpson is also suggestive of the hyracoids. The long, slender, and nearly straight ilium with the little-developed anterior inferior spine adjacent to the acetabulum is decidedly unlike *Meniscotherium*. I note that the calcaneum has a rather prominent peroneal tubercle and a large and rather elongate astragalar condyle, but the anterior portion of the bone is relatively short, although the astragalus has an elongate neck as in *Meniscotherium*. The sustentacular facet extends far forward on the neck of the astragalus, and the ectal facet is oval concave and nearly transverse, somewhat more as in *Tetraclaenodon* in this latter respect. Simpson regarded the presence of an astragalar foramen in *Pleuraspidotherium* as distinctive. We now know, however, that this foramen is present in the astragalus of *Meniscotherium* as well.

*Orthaspidotherium* offers many more problems in its comparison with *Meniscotherium*, and the character of the lower teeth is rather inconsistent with any rather close relationship to *Pleuraspidotherium*. Their artiodactyl-like structure is rather striking. A close relationship to *Pleuraspidotherium* has been postulated on the close resemblance of the upper teeth. An interpretation of homologies of cusps of the upper teeth suggested by Simpson would not be inconsistent with a supposition of artiodactyl affinities for *Orthaspidotherium*. Nevertheless, foot bones attributed to *Orthaspidotherium* by Teilhard de Chardin, if correctly assigned, would scarcely be compatible with an artiodactyl relationship.

It has been suggested to me that possibly *Protoselene* is ancestral to *Meniscotherium*. In a comparison of these two it would seem that the teeth of *Protoselene* possess a distinct potentiality for such a development. Nevertheless, the change required is rather striking in degree for an interval such as between Torrejonian or early Tiffanian

and Clarkforkian Paleocene. The fourth premolars above and below show no approach toward the molariform condition observed in *Meniscotherium*. The outer wall of the upper molars shows some tendency toward the styler condition in the latter, but the accessory cuspules are situated on the crests or horns of the protocone. In *Meniscotherium* these cuspules are distinctly separated from the protocone, with the protoconule independently crescentic and the metaconule aligned in a crest with the hypocone. Moreover, the distinct cingulum around the protocone of *Meniscotherium* is missing in *Protoselene*. The lower molars would seem to possess an equivalent potentiality, but the trigonid is comparatively short and the paraconid arm or crest has become rather abbreviated in the earlier form. Possibly *Protoselene* is better situated in time and in the character of the accessory cuspules of the upper molars for a possibly closer affinity to the litopterns than are any of the other North American Paleocene condylarths.

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## EXPLANATION OF PLATES

### PLATE 1. *Meniscotherium* skull from the early Eocene of Wyoming

#### *Meniscotherium chamense* Cope

Skull (U.S.N.M. 22672), dorsal, lateral, and ventral views. Natural size.  
New Fork member, Wasatch formation, Green River Basin, Wyo.

### PLATE 2. *Meniscotherium* skull from the early Eocene of Wyoming

#### *Meniscotherium robustum* Thorpe

Skull (U.S.N.M. 18260), dorsal, lateral, and ventral views.  $\frac{3}{4}\times$  natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

### PLATE 3. *Meniscotherium* skull from the early Eocene of Wyoming

Figs. 1, 2. *Meniscotherium chamense* Cope. 1, Skull and mandible (U.S.N.M. 22918), lateral view. Natural size. 2, Basicranium (U.S.N.M. 22672), ventral view.  $2\times$  natural size. New Fork member, Wasatch formation, Green River Basin, Wyo. Explanation of abbreviations follows:

- a.c., alisphenoid canal.
- e.a.m., position of external auditory meatus.
- f.l.m., foramen lacerum medium.
- f.l.p., foramen lacerum posterius.
- f.o., foramen ovale.
- fen. o., fenestra ovalis.
- fen. r., fenestra rotundum.
- gl., glenoid surface.
- h.f., hypoglossal foramen.
- p.gl.f., postglenoid foramen.
- p. gl.p., postglenoid process.
- p.p., paroccipital process.
- VII., aperture in facial canal for facial nerve.

### PLATE 4. *Meniscotherium* type specimens

Fig. 1. *Meniscotherium robustum* Thorpe. Skull and mandible (Y.P.M. 10101), type specimen, lateral view.  $\frac{2}{3}\times$  natural size. Left upper cheek teeth (Y.P.M. 10101), type specimen, occlusal view. Natural size. Aspen, Knight member, Wasatch formation, Green River Basin, Wyo.

Fig. 2. *Meniscotherium terraerubrae* Cope. Maxilla and jaw portion (A.M. 4410), type specimen, occlusal view of upper teeth, lateral and occlusal view of lower jaw fragment. Natural size. San José formation, San Juan Basin, N. Mex.

Fig. 3. *Meniscotherium tapiacitis* Cope. Lower jaw portions (A.M. 4425), type specimen, lateral and occlusal views. Natural size. San José formation, San Juan Basin, N. Mex.

Fig. 4. *Meniscotherium chamense* Cope. Right maxilla (U.S.N.M. 1093), type specimen, occlusal view. Natural size. San José formation, San Juan Basin, N. Mex.

PLATE 5. *Meniscotherium* dentitions from the early Eocene of Wyoming

Figs. 1, 2. *Meniscotherium robustum* Thorpe. 1, Left upper dentition, I<sup>1</sup>, C, P<sup>2</sup>—M<sup>3</sup> (U.S.N.M. 18314), occlusal view. 2, Right ramus of mandible, P<sub>3</sub>—M<sub>3</sub> (U.S.N.M. 18314), occlusal and lateral views. 1½× natural size. La Barge, Green River Basin, Wyo.

Figs. 3, 4. *Meniscotherium chamense* Cope. 3, Left upper dentition I<sup>3</sup>—M<sup>3</sup> (U.S.N.M. 22435), occlusal view. 4, Left ramus of mandible, I<sub>2</sub>—M<sub>3</sub> (U.S.N.M. 22435), occlusal and lateral views. 1½× natural size. New Fork, Green River Basin, Wyo.

Figs. 5, 6. *Meniscotherium tapiacitis* Cope. 5, Right maxilla, P<sup>3</sup>, M<sup>1</sup>—M<sup>2</sup> (U.S.N.M. 22431), occlusal view. 6, Right ramus of mandible, M<sub>1</sub>—M<sub>2</sub> (U.S.N.M. 22432), occlusal and lateral views. 1½× natural size. Bitter Creek, Washakie Basin, Wyo.

PLATE 6. *Meniscotherium* humerus and scapula  
from the early Eocene of Wyoming

Figs. 1, 2. *Meniscotherium robustum* Thorpe. 1, Right humerus (U.S.N.M. 19555, restored from U.S.N.M. 19519 and 19556), lateral, posterior, distal, proximal, and medial views. 2, Left scapula (U.S.N.M. 18314), proximal and lateral views. Natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

PLATE 7. *Meniscotherium* fore limb and foot material from the early Eocene

Figs. 1–10. *Meniscotherium chamense* Cope. 1, Right humerus (U.S.N.M. 22672), anterior and medial views. 2, Left radius (U.S.N.M. 22435), anterior and lateral views. 3, Left ulna (U.S.N.M. 22435), anterior and lateral views. 4–7, Articulated right carpus (U.S.N.M. 22672, pisiform introduced from U.S.N.M. 22918, and trapezoid from Y.P.M. 10276); 4, proximal view; 5, distal view; 6, lateral view; and 7, medial view. 8, Left metacarpals I–V (I, U.S.N.M. 18314; II–IV, U.S.N.M. 22672; V (reversed), U.S.N.M. 22918), proximal view of bases. 9, Articulated, partially composite, right manus, excluding phalanges (U.S.N.M. 22672, except pisiform introduced from U.S.N.M. 22918, trapezoid from Y.P.M. 10276, and metacarpals I (reversed), U.S.N.M. 18314, and V, U.S.N.M. 22918 (II–IV of 22672 reversed)), dorsal view. 10, Phalanges of digit II or IV (U.S.N.M. 22918), dorsal view. All natural size.

Fig. 11. *Meniscotherium robustum* Thorpe. Distal phalanx of manus (U.S.N.M. 18282), dorsal view.

PLATE 8. *Meniscotherium* femur and patella from the early Eocene of Wyoming

Figs. 1, 2. *Meniscotherium robustum* Thorpe. 1, Right femur (U.S.N.M. 18283), posterior, distal, medial, proximal, and anterior views. 2, Patella (U.S.N.M. 18283), anterior view. Natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

PLATE 9. *Meniscotherium* tibiae and fibula from the early Eocene of Wyoming

Fig. 1. *Meniscotherium robustum* Thorpe. Right tibia and fibula (U.S.N.M. 18283), proximal, lateral, anterior, and distal views. Natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

Fig. 2. *Meniscotherium*, cf. *chamense* Cope. Right tibia (U.S.N.M. 22675, restored from U.S.N.M.: 22672), anterior and lateral views. Natural size. New Fork member, Wasatch formation, Green River Basin, Wyo.

PLATE 10. *Meniscotherium* pedes from the early Eocene

Figs. 1-4. *Meniscotherium chamense* Cope. 1, Left navicular (U.S.N.M. 22918) and left cuboid (Y.P.M. 20950), proximal and distal views, and lateral view of navicular.  $1\frac{1}{2}\times$  natural size. Navicular from New Fork member, Wasatch formation, Green River Basin, Wyo. Cuboid from San José formation, San Juan Basin, N. Mex. 2, Left pes (U.S.N.M. 22435, with cuboid restored from Y.P.M. 20950), medial and dorsal views. Natural size. New Fork member, Wasatch formation, Green River Basin, Wyo. (except cuboid from San Juan Basin). 3, Metatarsals I-V (I, V, U.S.N.M. 22918; II, Y.P.M. 20949; III, Y.P.M. 20948; IV, Y.P.M. 10559), proximal view of bases  $1\frac{1}{2}\times$  natural size. Metatarsals I and V from New Fork member, Wasatch formation, Green River Basin, Wyo. Metatarsals II-IV from San José formation, San Juan Basin, N. Mex. 4, Left calcaneum and right astragalus (U.S.N.M. 22918), dorsal and ventral views respectively.  $1\frac{1}{2}\times$  natural size. New Fork member, Wasatch formation, Green River Basin, Wyo.

Figs. 5-8. *Meniscotherium robustum* Thorpe. 5, Left external cuneiform (U.S.N.M. 18283), proximal, medial, and distal views.  $1\frac{1}{2}\times$  natural size. 6, Left pes (U.S.N.M. 18282, lacking 1st and 5th digits and distal phalanges), dorsal view. Natural size. 7, Second phalanx, 3d(?) digit (U.S.N.M. 18283, dorsal and lateral views.  $1\frac{1}{2}\times$  natural size. 8, Distal phalanx, 3d(?) digit (U.S.N.M. 18283), dorsal, lateral and ventral views.  $1\frac{1}{2}\times$  natural size. La Barge, Knight member, Wasatch formation, Green River Basin, Wyo.

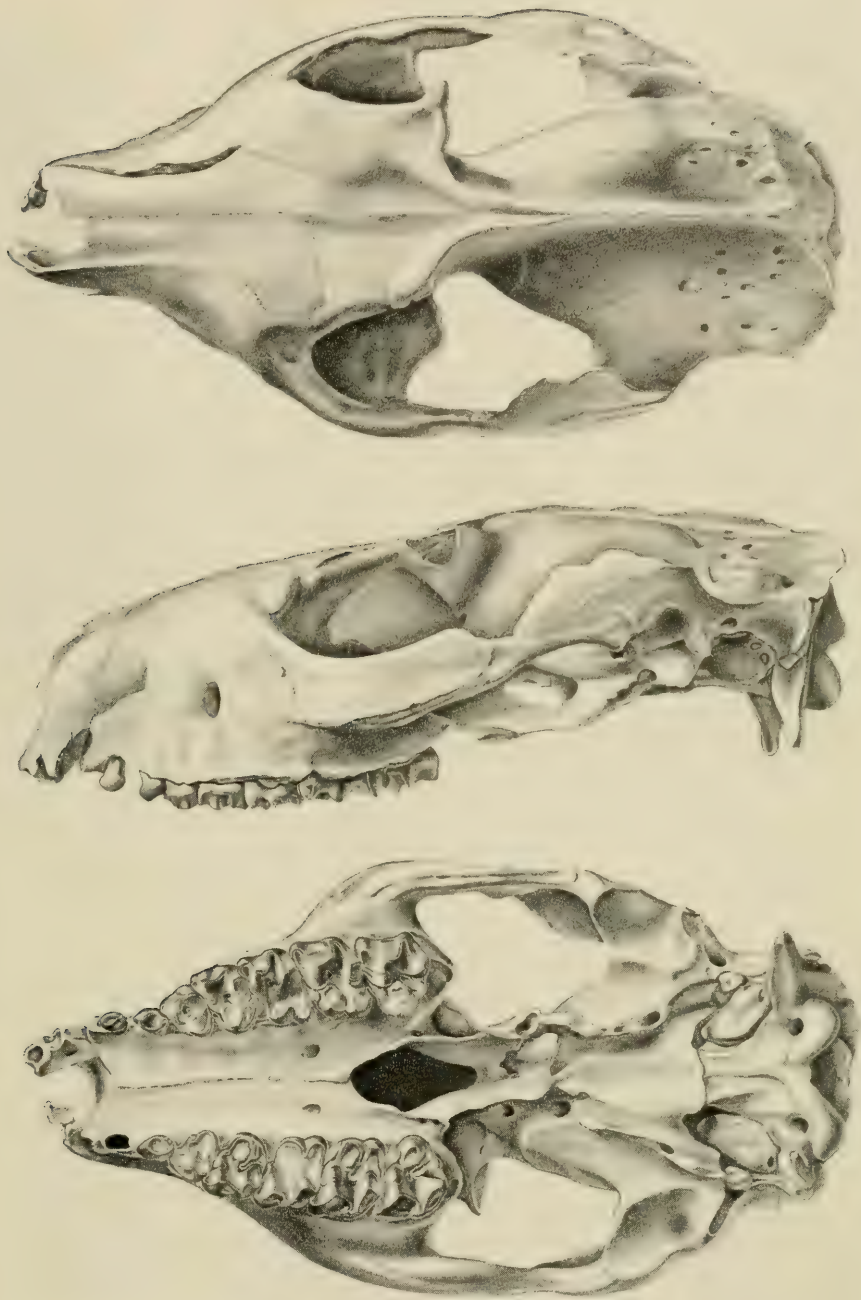
PLATE 11. Restoration of *Meniscotherium*

Restoration of *Meniscotherium* by the artist Walter Ferguson based on a composite skeleton from the San Juan Basin of New Mexico. Photograph by courtesy of the American Museum of Natural History.

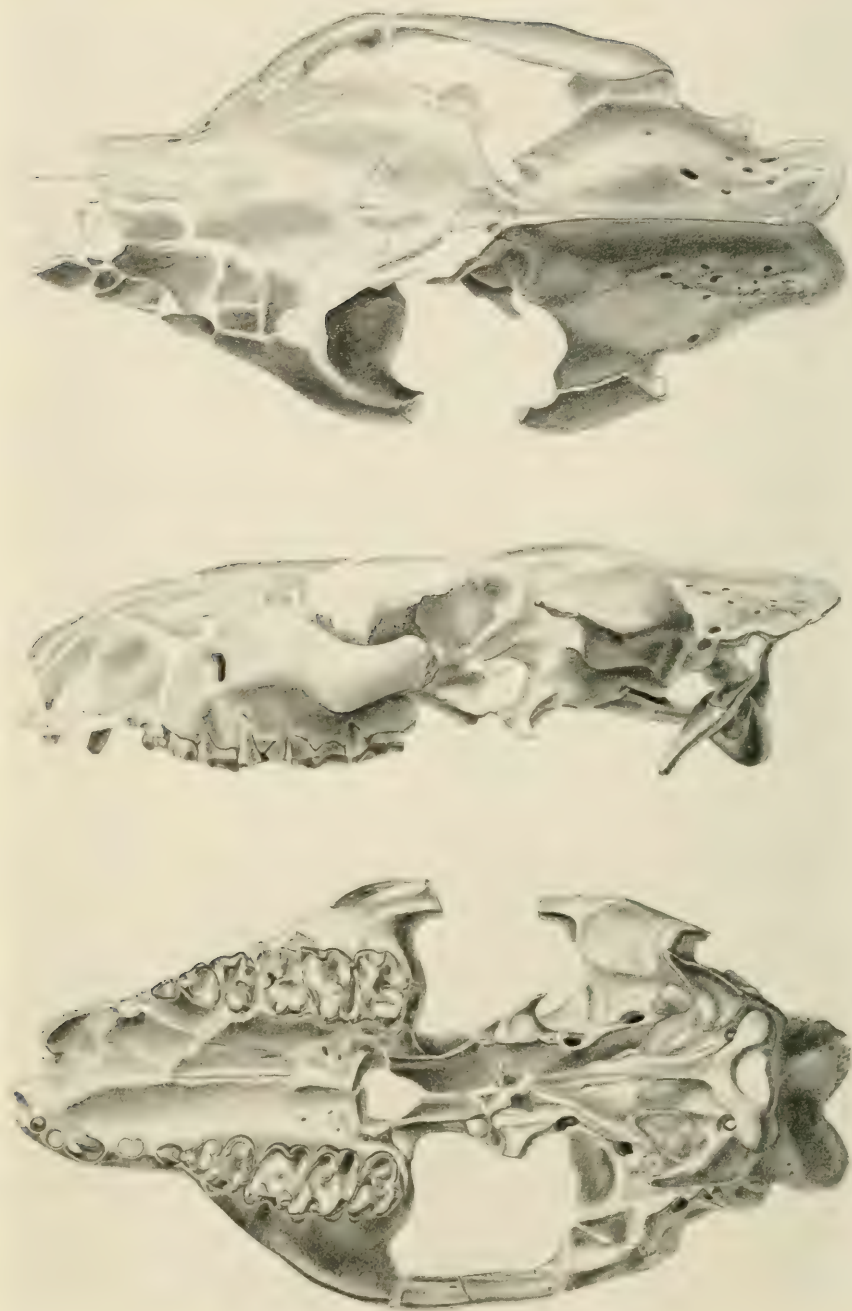
## PLATES







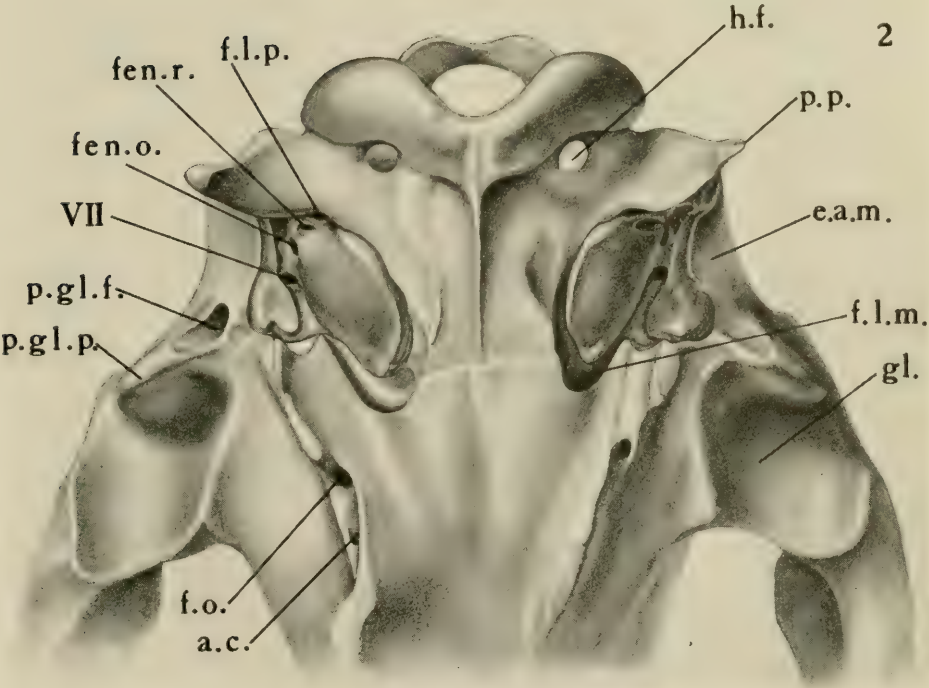
Meniscotherium skull from the early Eocene of Wyoming  
(See explanation of plates at end of text.)



Meniscotherium skull from the early Eocene of Wyoming  
(See explanation of plates at end of text.)



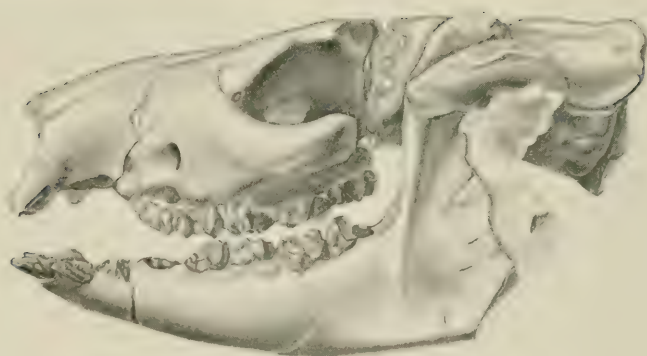
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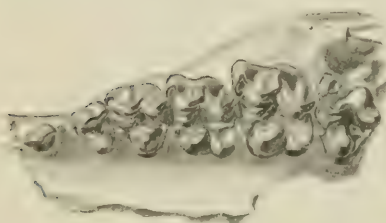
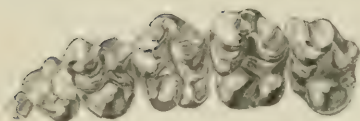
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Meniscotherium skull from the early Eocene of Wyoming  
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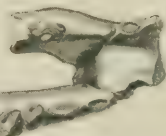
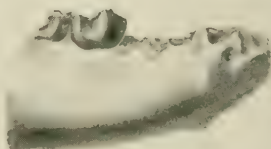




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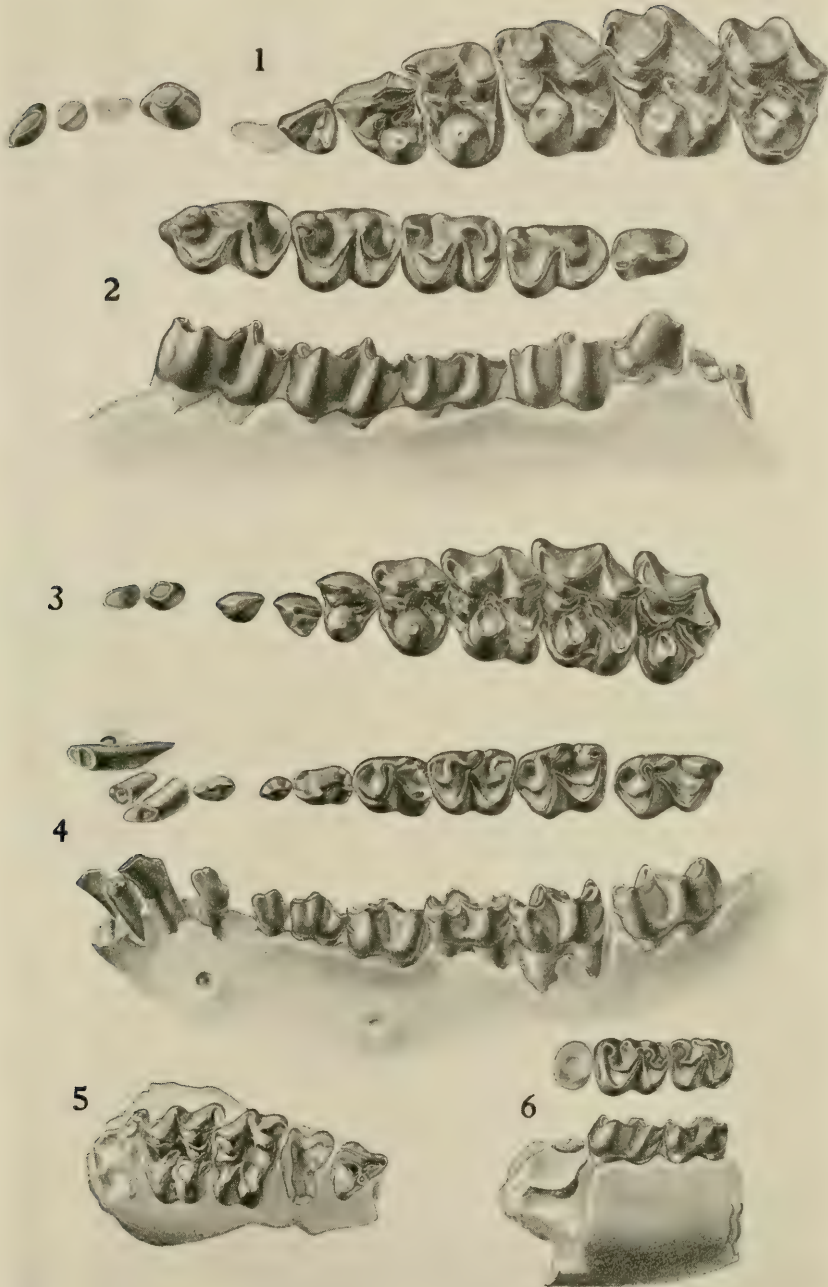
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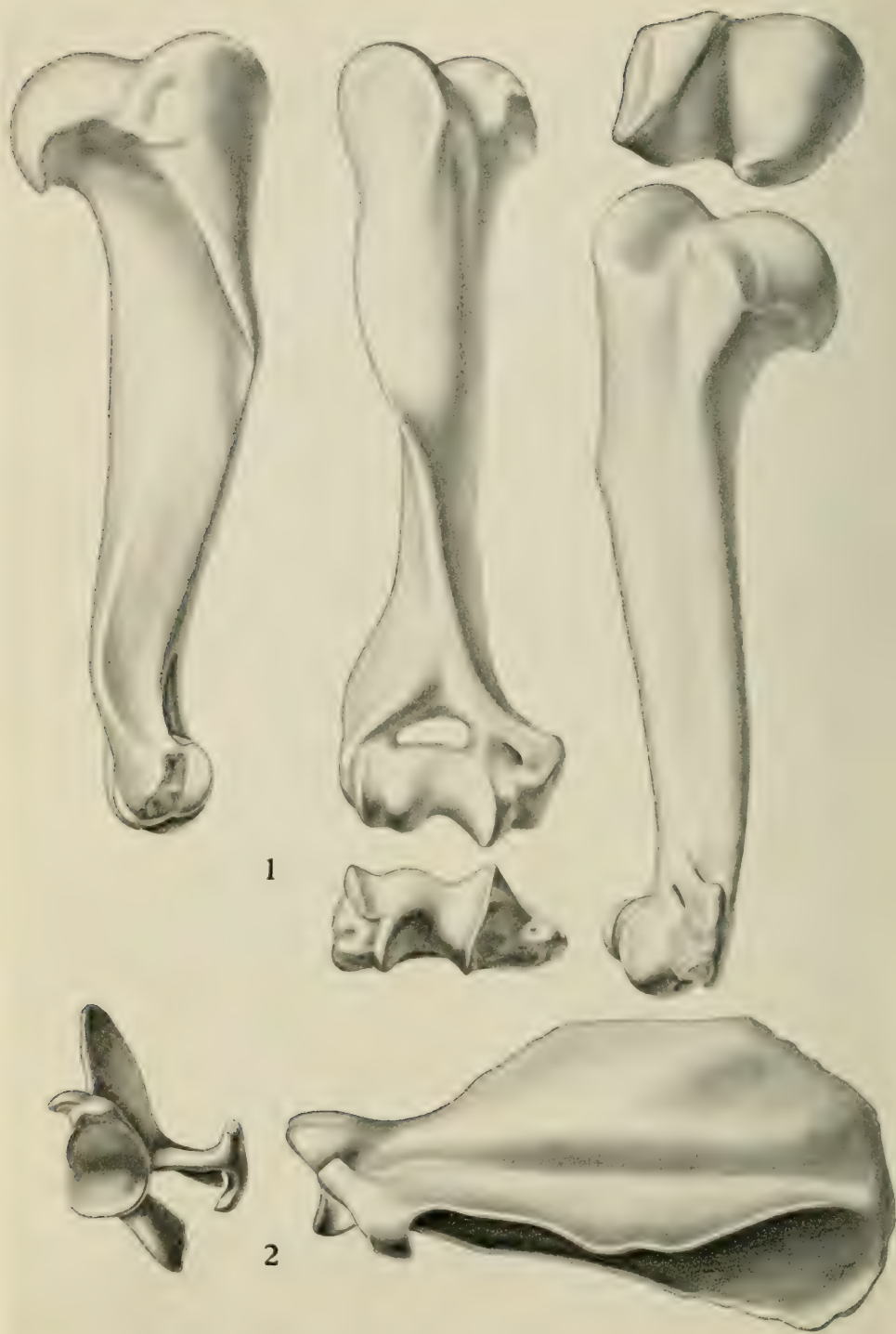
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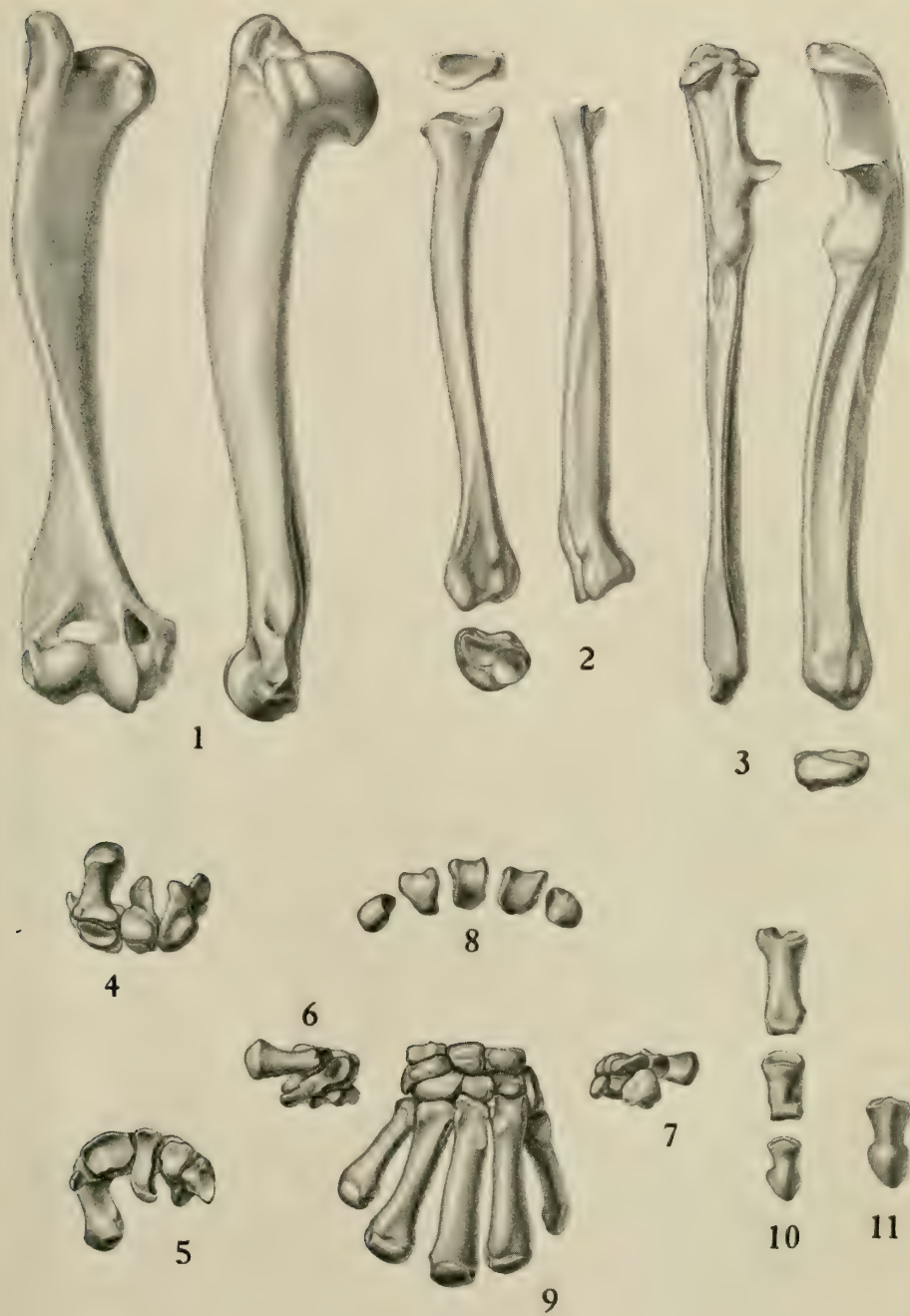
Meniscotherium type specimens  
(See explanation of plates at end of text.)



Meniscotherium from the early Eocene of Wyoming  
(See explanation of plates at end of text.)

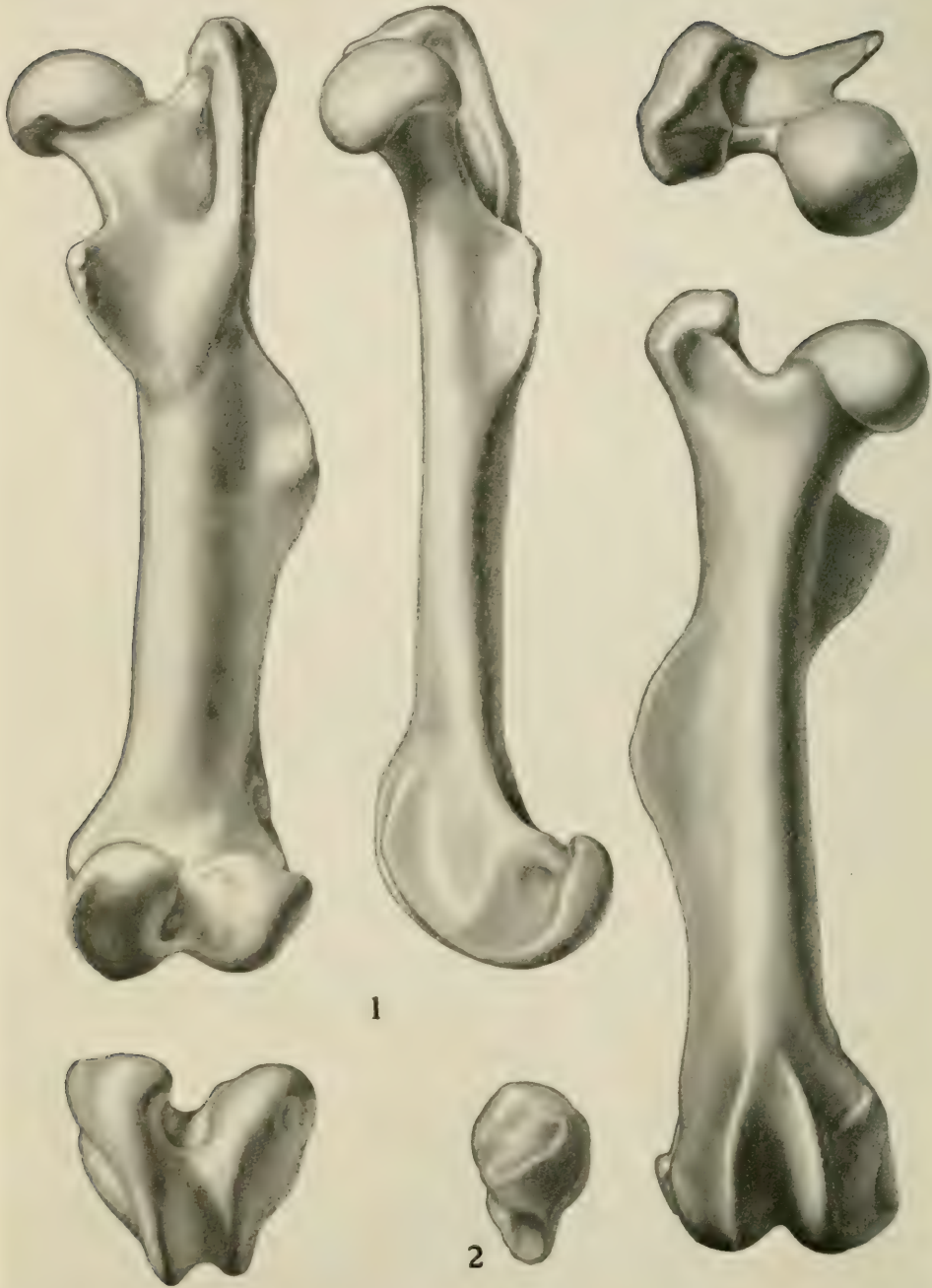


Meniscotherium humerus and scapula from the early Eocene of Wyoming  
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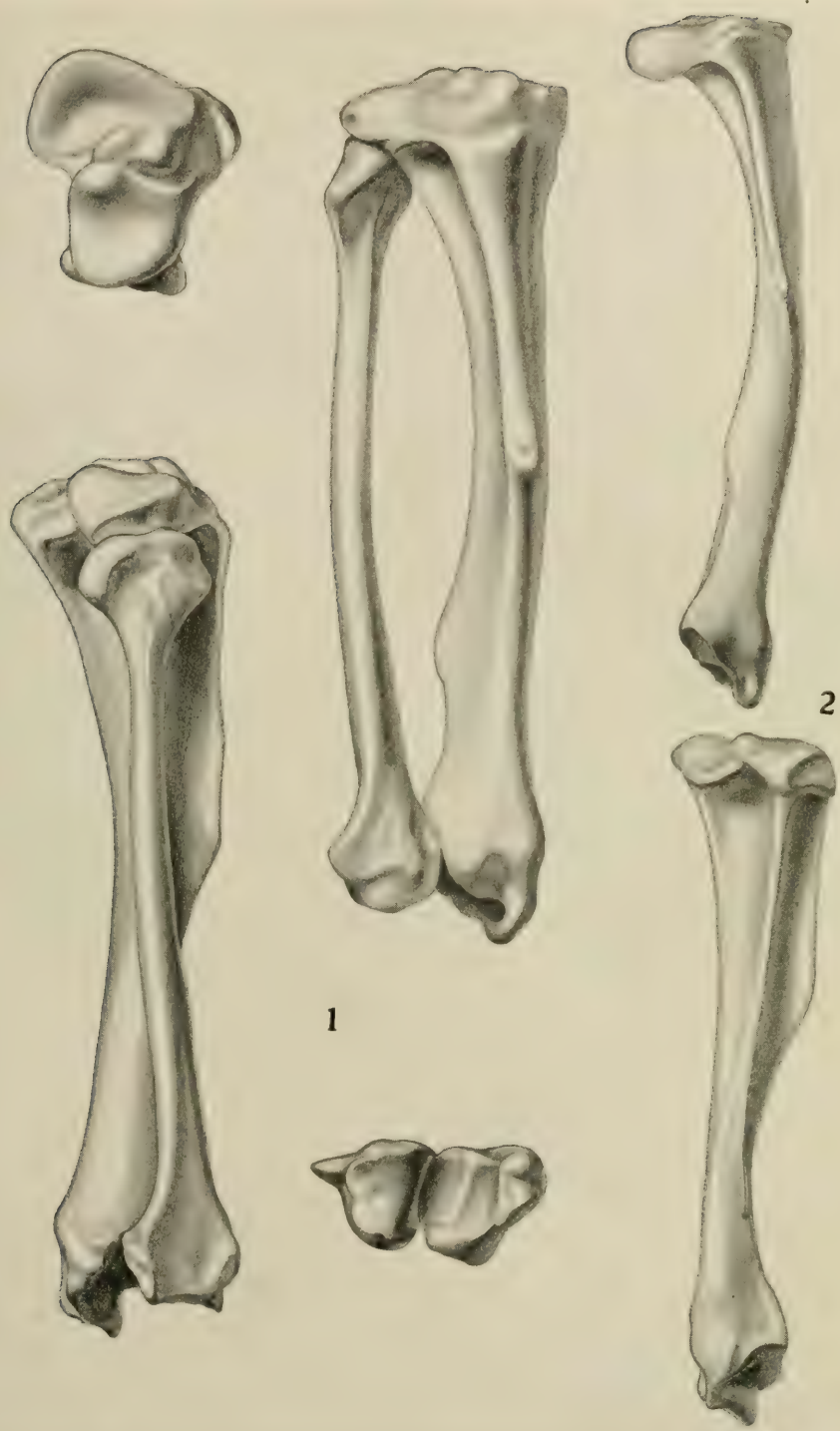


*Meniscotherium* fore limb and foot material from the early Eocene  
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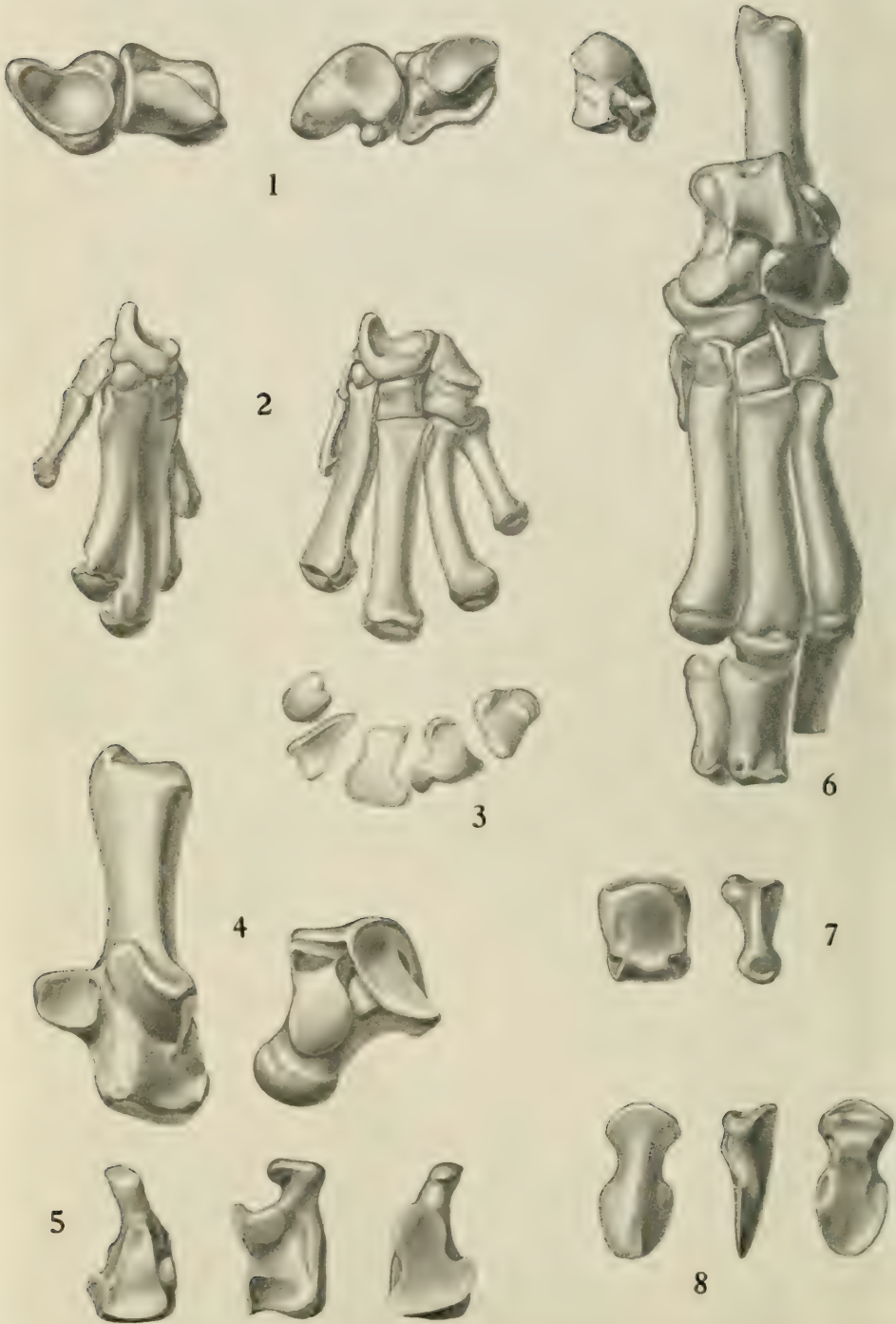




Meniscotherium femur and patella from the early Eocene of Wyoming  
(See explanation of plates at end of text.)



Meniscotherium tibiae and fibula from the early Eocene of Wyoming  
(See explanation of plates at end of text.)



Meniscotherium pedes from the early Eocene  
(See explanation of plates at end of text.)



Restoration of *Meniscotherium*  
(See explanation of plates at end of text.)









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THE RELATIONSHIPS OF QUEMISIA  
GRAVIS  
(RODENTIA: HEPTAXODONTIDAE)

(WITH ONE PLATE)

By

CLAYTON E. RAY

Associate Curator, Division of Vertebrate Paleontology  
U. S. National Museum  
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The large Hispaniolan caviomorph *Quemisia gravis* was described by G. S. Miller, Jr. (1929a, pp. 22-25; pl. 4, figs. 2, 2a) on the basis of a fragmentary immature right mandibular ramus (the type, U.S.N.M.<sup>1</sup> 253175), a fragment of an upper incisor, and a partial femur, all from caves near St. Michel de L'Atalaye in north-central Haiti. To these Miller added later in the same year (1929b, pp. 10-11, pl. 2, fig. 3) a distal half of a femur and the proximal end of an ulna, both from a cave at Boca del Infierno on the southern shore of Bahia de Samana, Dominican Republic. These five fragments constitute the entire known material of *Quemisia*, and of them only the jaw is of much value in determining the affinities of the genus.

In the initial description and subsequently—insofar as it has been noticed at all—*Quemisia* has been associated closely with *Elastodontomys*. G. M. Allen, the only author aside from Miller who has done more than incorporate *Quemisia* into a survey or checklist, stated (1942, p. 128) that Schreuder's (1933) specimens of *Amblyrhiza* "indicate that the animal was closely allied to the 'Quemi' of Santo Domingo, with essentially the same enamel pattern of the molars but with a relatively longer rostrum. . . . The animal must have been a giant in comparison with the 'Quemi'." <sup>2</sup> How-

<sup>1</sup> U.S.N.M. stands for United States National Museum, M.C.Z. for Museum of Comparative Zoology, and A.M.N.H. for American Museum of Natural History.

<sup>2</sup> The generic name *Quemisia* reflects Miller's supposition that the animal was the "Quemi" of Oviedo, whose brief description of the animal not actually seen by him was quoted by MacLeay (1829, p. 275) and by Miller (1929b,



ever, except for a fragment of a lower incisor 50 mm. in length, Schreuder had only cranial fragments and the upper dentition of *Amblyrhiza*, all of which were mature, whereas, except for the three postcranial scraps and a fragment of an upper incisor 19 mm. in length, *Quemisia* is known only from an immature lower jaw. Obviously, close comparison between *Quemisia* and Schreuder's specimens of *Amblyrhiza* is impossible, and, although mandibular material of *Amblyrhiza* is available, the closely related *Elasmodontomys* can be more usefully compared to *Quemisia* in that the two are known from jaws of comparable ontogenetic age and are similar in size.

In fact, however, in most characters except size and some details of dentition, *Quemisia* is dissimilar to *Elasmodontomys* and similar to the Capromyidae, in particular to *Plagiodontia* (figs. 1, 2). Interestingly, most of the features in which *Quemisia* differs from *Elasmodontomys* were well described by Miller, who nevertheless failed to recognize that these very features seem to ally *Quemisia* with the Capromyidae. Most of the comparisons of *Quemisia* with *Elasmodontomys* and *Plagiodontia* are straightforward and are most readily comprehended in tabular form (table 1).

The interpretation of the enamel configuration of the cheekteeth, however, is more complex and requires some discussion. The occlusal surface of each cheektooth in *Quemisia* is dominated by three deep, narrowly compressed reentrant folds, two lingual (anterior) and one labial (posterior). The lingual reentrants extend to or almost to the opposite, external enamel wall but do not breach it (except very shallowly in the anterior fold of the unworn  $M_3$ ). The labial reentrant is completely penetrant, producing on the occlusal surface an isolated posterior enamel island. However, the depth of penetration on the lingual wall by this reentrant is very shallow, especially in the first cheektooth, so that with slight additional wear this fold would have assumed the character of the lingual ones. In *Elasmodontomys* the lingual reentrants are completely penetrant apically, as is the labial reentrant, thus generally producing in moderately worn permanent lower cheekteeth a pattern of four obliquely oriented complete enamel ellipses succeeding

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p. 13) and Latinized by Fischer (1830, p. 389[=589]) as *C.[=Capromys] quemi*. Allen (1942, p. 128) pointed out that if Miller's supposition were correct, then the scientific name should be *Quemisia quemi*. However, it seems highly improbable that the identity of Miller's *Quemisia* with Oviedo's "Quemi" could ever be established beyond reasonable doubt. Thus, *Quemisia quemi* is best regarded as a nomen dubium.

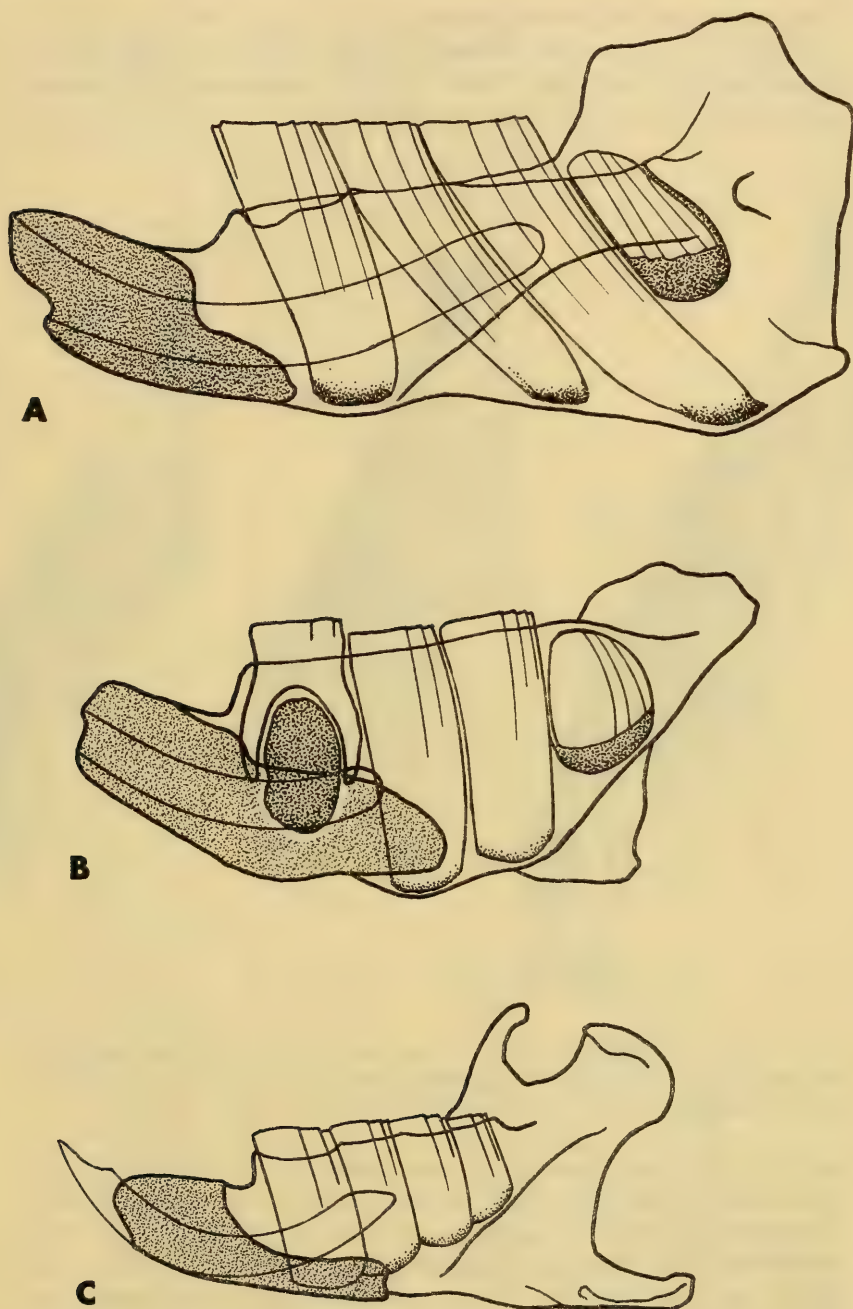


FIG. 1.—Right mandibular rami in lingual aspect of (A), *Elasmodontomys obliquus*, A.M.N.H. 17137h; (B), *Quemisia gravis*, U.S.N.M. 253175 (the type); (C), *Plagiodontia hylaeum*, M.C.Z. 35314. Diagrammatically represented, largely on the basis of X-ray photographs.  $1\frac{1}{2} \times$  natural size.

one another on the occlusal surface, as in  $P_4$  of A.M.N.H. 17137h (fig. 2A). With varying amounts of additional wear the lingual folds generally withdraw from complete penetrance but remain tightly appressed or in close approximation to the external enamel

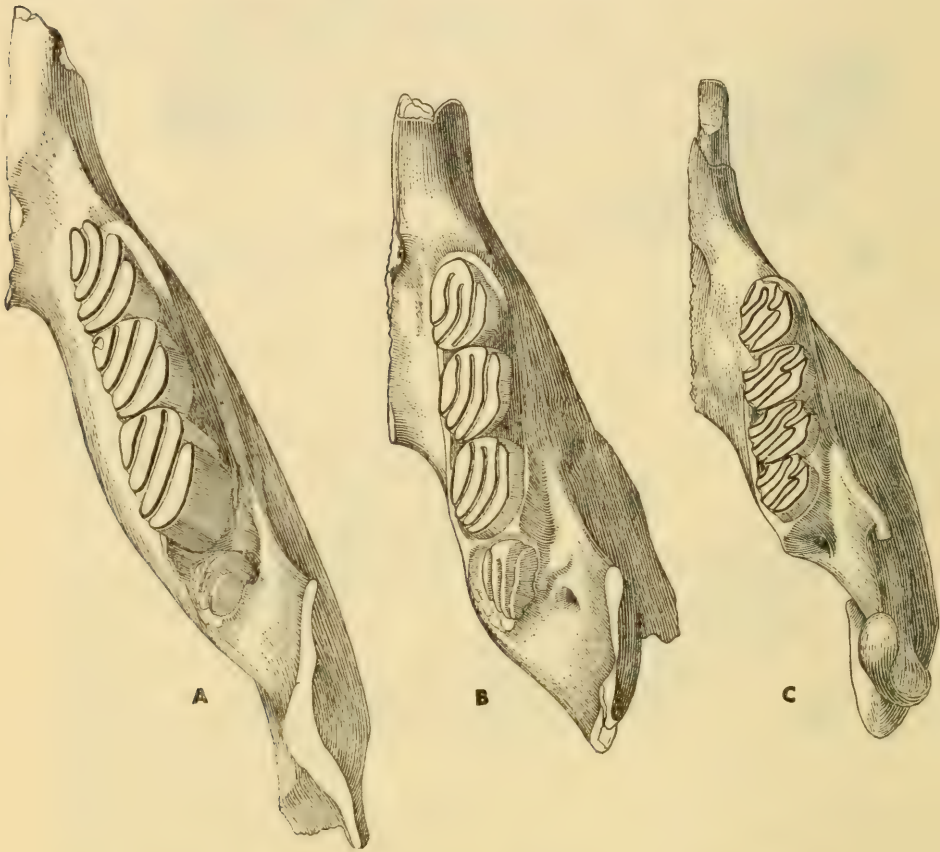


FIG. 2.—Right mandibular rami in occlusal aspect of (A), *Elasmodontomys obliquus*, A.M.N.H. 17137h; (B), *Quemisia gravis*, U.S.N.M. 253175 (the type); (C), *Plagiodontia hylaeum*, M.C.Z. 35314.  $1\frac{1}{2} \times$  natural size.

wall of the tooth through extreme wear, as in  $M_1$  and  $M_2$  of A.M.N.H. 17137h (fig. 2A). The labial reentrant generally remains completely penetrant in deeply worn teeth. The dentition of *Elasmodontomys* in general is discussed in detail by Ray (1964b). One labial and two (major) lingual reentrant folds are present in the lower cheekteeth of *Plagiodontia* and other Antillean capromyids.



TABLE 1.—*Comparison of Quemisia with Elasmodontonys and Plagiodontia.*

All quoted passages are from Miller (1929a, pp. 22-24). In order to facilitate comparison to specimens not X-rayed, the posterior termination of the mandibular symphysis and of the incisor is expressed in relation to the occlusal plane of the cheekteeth, by projection of the termini perpendicular to that plane, with the line of sight perpendicular to the symphyseal (midsagittal) plane.

<i>Elasmodontonys</i>		<i>Quemisia</i>		<i>Plagiodontia</i>
1. Size large. Occlusal length $P_1-M_2$ , 27.6 mm.	1. Size large. Occlusal length $DP_1-M_2$ , 24.5 mm.	1. Size medium. Occlusal length $DP_1-M_2$ , 15.7 mm. in M.C.Z. 35314, an adult; less in younger individuals.	1. Size medium. Occlusal length $DP_1-M_2$ , 15.7 mm. in M.C.Z. 35314, an adult; less in younger individuals.	
2. "Mandibular symphysis extending . . . barely to middle of pm."	2. "Mandibular symphysis extending backward beyond level of middle of $m_1$ ," actually to posterior margin of $M_1$ . The great breadth of the symphysis undoubtedly is correlated with large size.	2. Mandibular symphysis extending to posterior edge of $DP_1$ even in specimens much younger than <i>Quemisia</i> and to posterior margin of $M_1$ in adults.	2. Mandibular symphysis extending to posterior edge of $DP_1$ even in specimens much younger than <i>Quemisia</i> and to posterior margin of $M_1$ in adults.	
3. "Shaft of the incisor extends far beyond the symphysis to terminate beneath middle of $m_2$ ," actually beneath posterior margin of $M_2$ .	3. "Shaft of lower incisor not extending behind symphysis, its base lying beneath anterior half of $m_1$ ," actually beneath middle of $M_1$ .	3. Shaft of lower incisor extending little or not at all behind symphysis, its base lying beneath middle of $M_1$ .	3. Shaft of lower incisor extending little or not at all behind symphysis, its base lying beneath middle of $M_1$ .	
4. Angular process not flaring laterad, lying in plane of cheekteeth; dentigerous portion of mandible continuous with angular process, which "is so thick that it forms considerably more than half of the entire transverse diameter" of the mandible.	4. Angular process flaring laterad, offset from plane of cheekteeth; dentigerous portion of mandible "separated from the base of the angular process by a shallow groove. . . . Anterior base of the angular process . . . laterally compressed . . . so that it forms about one-third of the transverse diameter of the mandible."	4. Angular process as in <i>Quemisia</i> .	4. Angular process as in <i>Quemisia</i> .	



TABLE 1. Continued

*Elasmodontomys*

5. Horizontal and ascending rami of mandible lying in same plane, lingual surfaces merging over broad area.

6. Mandibular foramen opening on lingual surface of jaw posterior to tooththrow, in typical mammalian position.

7. Molars invading thickened angular process (cf. 4 above), penetrating to its ventral border; extremely hypsodont; forming roots; maximum height of  $M_2$  (38.6 mm.) much greater than occlusal length of  $P_1-M_2$  (cf. 1 above).

8.  $P_1$  locus diphyodont;  $DP_1$  replaced prior to eruption of  $M_2$ .

9. Cheektooth row oblique to sagittal plane.

*Quemisia*

5. Horizontal and ascending rami offset, lingual surfaces with bony ridge extending posterodorsad from directly behind the last molar toward the articular process, decreasing in height posterodorsally and merging with ascending ramus.

6. Mandibular foramen opening on dorsal face of horizontal ramus between  $M_2$  and ascending ramus.

7. Molars not invading angular process (cf. 4 above); moderately hypsodont; probably evergrowing; maximum height of  $M_2$  (21.3 mm.) less than occlusal length of  $DP_1-M_2$  (cf. 1 above).

8.  $P_1$  locus diphyodont;  $DP_1$  replaced subsequent to eruption of  $M_2$ .

9. Cheektooth row almost parallel to sagittal plane.

*Plagiodontia*

5. Horizontal and ascending rami as in *Quemisia*.

6. Mandibular foramen opening as in *Quemisia*. (Little weight can be attached to this character as the condition in *Amblyrhiza* is somewhat similar to that in *Quemisia*.)

7. Molars as in *Quemisia*; cheekteeth definitely evergrowing; maximum height of  $M_2$  (11.6 mm. in M.C.Z. 35314) less than occlusal length of  $DP_1-M_2$  (cf. 1 above). In U.S.N.M. 253155, a younger individual, height of  $M_2$  is 12.0 mm., occlusal length of  $DP_1-M_2$ , 14.7 mm.

8.  $P_1$  locus monophyodont;  $P_1$  probably suppressed.

9. Cheektooth row oriented as in *Quemisia*.

In these forms the labial reentrant lies anterior to the posterior lingual one (*Plagiodontia*, *Capromys*), abuts it (*Isolobodon*), or merges with it (*Aphaetreus*). An isolated posterior enamel island is thus produced in *Aphaetreus*, superficially as in *Quemisia* but actually through the confluence of two folds, not the complete penetration of one. The lingual folds in *Plagiodontia* and the labial fold in *Isolobodon* and *Aphaetreus* approach those of *Quemisia* most closely in compression and depth of penetration, and although the approach is not very close, it is not so remote in this respect as are these genera from *Capromys*.

The posterior enamel wall of each reentrant fold in *Quemisia* is extremely thin and in places not certainly detectable owing to damage to the occlusal surface. Similar, but less radical, thinning is characteristic of *Elasmodontomys* but has been observed in no Antillean capromyid.

Among the most striking features of *Quemisia*, Miller (1929a, p. 24) noted that "the forward turning of the enamel folds so that the anterior portion of each fold is approximately parallel with the main axis of the tooththrow is a specialization of high degree and very peculiar kind." This character is especially well shown by a sharp flexure of the posterior (here posterolabial) wall of each tooth, marking the "forward turning." A similar flexure is present on the corresponding face in *Plagiodontia*, but it is not well shown by the reentrants. Differences in enamel configuration between *Quemisia* and *Plagiodontia* appear to be no greater than between the latter and *Capromys*.

The discovery of a new species of capromyid (Ray, 1964a), assigned tentatively to *Plagiodontia* and based unfortunately on a single tooth (DP<sup>4</sup>?), narrows the structural gap between the dentition of *Quemisia* and that of capromyids. The new species has the crown of the tooth compressed perpendicular to the reentrant folds, and the deeply penetrant, much compressed reentrant folds oriented strongly anteroposteriorly.

As part of a general survey of Antillean capromyids, the above comparisons and those presented in table 1 were written in essentially their present form on the basis of the type description of *Quemisia gravis* at a time when the type specimen was temporarily unavailable. Subsequent availability of the type has not materially altered these observations, but X-rays of it have augmented them startlingly (fig. 1B). The first cheektooth is a deeply worn DP<sub>4</sub> with long slender anterior and posterior roots curving about a

large crypt for  $P_4$ . Judging from degree of wear of  $DP_4$  and state of development of  $M_3$ , the latter would have come into use prior to replacement of  $DP_4$  by  $P_4$ . In any case  $DP_4$  was retained relatively much longer in *Quemisia* than in *Elasmodontomys*. In a specimen of the latter with  $DP_4$  and the crypt for  $P_4$  in a condition comparable to that in the type of *Quemisia gravis*,  $M_2$  is just at the point of eruption (cf. Ray, 1964b, fig. 1D) and, in a specimen with  $M_3$  at the point of eruption (as in *Quemisia*),  $P_4$  is already in full use (fig. 1A).

I have examined the fragmentary upper incisor and the fragmentary femur referred to *Quemisia* from the caves near St. Michel de L'Atalaye and find in them no clues to the relationships of the genus. The femur is distinctive in the extreme flattening of the shaft (noted by Miller 1929a, p. 24) and in the relatively large size of the head (pl. 1). The referred specimens from Boca del Infierno could not be located at the time of this writing.

From the evidence at hand, I find only modest support for inclusion of *Quemisia* with the Heptaxodontinae and much to warrant exclusion. Similar size and geographic proximity afford only peripheral evidence of affinity with *Elasmodontomys*. The similarities noted in occlusal pattern and in enamel thinning constitute perhaps the most compelling evidence for relationship. Diphyodonty at the  $P_4$  locus is of course a primitive eutherian character retained in most other caviomorphs. Dental development at this locus in *Quemisia* differs in detail from that in heptaxodontines in the longer retention of  $DP_4$  in *Quemisia* (presaging suppression of  $P_4$ ?). The differences between *Quemisia* and *Elasmodontomys* in the preserved features of the lower jaw (table 1) indicate more radical divergence in their respective developmental complexes than that observed within caviomorph families.

The uncertain position of *Quemisia* emphasizes the eastern Caribbean distribution of heptaxodontines in that not only Cuba, but now perhaps Hispaniola, is without them. Furthermore, the relationships of the Jamaican *Clidomys*, *Speoxenus*, and *Spirodontomys*, customarily brigaded with the Heptaxodontinae, remain to be established. With regard to *Clidomys*, the best known of the three, Anthony (1920, p. 472) has wisely stated, "it would be premature to indulge in conjecture . . . as to the relationships of this new genus. It is significant, however, that the dentition shows *Clidomys* to be only remotely related to the other large hystricomorphs of the West Indies." In these statements I heartily concur, and, although pro-



nouncements on the detailed affinities of *Clidomys* must await careful study of specimens already available and the collection of supplementary material, there can be no doubt that, even if *Clidomys* should prove to be a heptaxodontid, its relationships to the eastern Caribbean forms are remote. Thus, the Heptaxodontinae at present include with certainty only *Amblyrhiza* on Anguilla and St. Martin, and *Elasmodontomys*<sup>3</sup> on Puerto Rico.

If *Quemisia* is not a heptaxodontine, then the only remaining probable relatives among Antillean caviomorphs are the capromyids. Of course, it is possible that *Quemisia* represents a separate invasion from the mainland and thus has no close Antillean relatives. This alternative is in my opinion the more radical and is unsupportable on the basis of present, admittedly meager, evidence. Prior to X-raying the mandible of *Quemisia*, I had confidently placed the genus in the family Capromyidae, comparing it most closely with *Plagiodontia*. Discovery of diphyodonty at the  $P_4$  locus in the specimen makes this assignment untenable at present, but evolutionarily much more interesting if correct. The transfer of *Quemisia* to the Capromyidae would disrupt not only the concept of that family but current superfamilial groupings as well (cf. Schaub, 1953, pp. 396-397; Wood, 1955, pp. 181-182; Wood and Patterson, 1959, pp. 323-327), which is not warranted on the basis of inadequate knowledge of a single genus. Pending discovery of more material, *Quemisia* may be retained, incertae sedis, in the Heptaxodontidae, recognizing that this is a temporary expedient.

Considering *Quemisia* for the moment as a capromyid, the impression is strengthened that Hispaniola has been an important center of capromyid radiation in the Antilles, in terms of both number of forms (five genera and nine species on Hispaniola) and breadth of diversification. The history of Antillean capromyid evolution assuredly is not a simple one of differentiation on and dispersal from Hispaniola or any one island, but *Plagiodontia*, *Isolobodon*, and *Aphaetreus* (with *Quemisia*?) do seem to constitute a natural assemblage (the *Plagiodontia* group), accounting for four genera and eight species on Hispaniola. The importance of this group in the Quaternary fauna of Hispaniola at least suggests origin of *Isolobodon* on that island, followed by eastward dispersal by natural means or human transport (or both) through Mona, Puerto Rico, St. Thomas, and St. Croix. The *Capromys* group (including *Capromys*, *Geo-*

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<sup>3</sup> *Heptaxodon* is based on juvenile individuals of *Elasmodontomys* and is the junior synonym (Ray, 1964b).



*capromys*, and *Hexolobodon*), represented on Hispaniola only by the well-differentiated *Hexolobodon phenax*, has its greatest diversity on Cuba with two genera, weakly differentiated, and five species.<sup>4</sup>

Available evidence suggests that the *Plagiodontia* group has undergone a relatively old radiation on Hispaniola but is not known with certainty to have dispersed from the island by natural means, whereas the *Capromys* group has undergone a relatively young radiation on Cuba and has dispersed widely from that island at least in part by natural means.

If *Quemisia* is in fact related to the capromyids, then it would suggest that the group has been in the Antilles longer and has undergone more extensive evolution there than previously would have been supposed. It is not impossible that Antillean caviomorphs have arisen from fewer, possibly older, invasions than their current taxonomic separation would imply, and that the descendants of a single invasion could in some cases have diverged to the familial level after invasion. On the basis of present evidence one can speculate at least that *Quemisia*, when better known, will provide an evolutionary bridge between Antillean capromyids and heptaxodontines.<sup>5</sup> Naturally, since all known forms are of Quaternary age, they must be regarded as collateral members of an adaptive radiation, none of which is ancestral to another, and all of which have evolved at differing rates both in the relation of one lineage to another and of one structure to another in a single lineage. Regarded as divergent products of a single adaptive radiation, the heptaxodontines are relatively highly evolved in terms of hypsodonty and enamel configuration, but conservative in retention of  $P_4$  diphyodonty and root formation in  $P_4-M_3$ , whereas the capromyids are more conservative in degree of hypsodonty and enamel modification, but advanced in the suppression of  $P_4$  and evergrowing cheekteeth. *Quemisia* presents a melange of highly evolved and conservative characters. If the relationships suggested here are real, the waif which gave rise to the Antillean capromyids and heptaxodontines must have dispersed from the mainland prior to the suppression of  $P_4$ . According to the interpreta-

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<sup>4</sup> Schaub (1953, pp. 396-397) distributes the genera discussed in this paragraph among four families, an arrangement which I am wholly unable to accept, but the analysis of which is outside the scope of this paper.

<sup>5</sup> Wood and Patterson (1959, pp. 325-326) have utilized the lateral process of the supraoccipital in drawing the Echimyidae and Capromyidae together but have pointed out with regret the strong development of the process in *Elasmodontomys*. Is it possible that the lateral process in *Elasmodontomys* is of more profound significance than merely another regrettable instance of rodent parallelism?

tions of Wood and Patterson (1959, pp. 301, 324-326), the invader would necessarily have been an echimyid (or protocapromyid) and the time pre-Colhuehuapian.<sup>6</sup> Persistence of  $P_4$  in some insular descendants perhaps would not be so startling as in mainland forms.

The above suggestions will remain highly speculative until cranial material of *Quemisia* and of Tertiary caviomorphs is discovered in the Antilles. Nevertheless, it is clear already that *Quemisia* is potentially of great importance in the interpretation of the history of Antillean caviomorphs and has bearing on the arrangement of the Caviomorpha as a whole. Further, it is increasingly clear that the large, high, complex island of Hispaniola will eventually yield the answers to many problems of Antillean faunal history.

I acknowledge with pleasure the assistance of David H. Johnson of the U. S. National Museum, who made available the extensive collections of fossil caviomorphs, including *Quemisia*, from the vicinity of St. Michel de L'Atalaye; Ernest Williams, Karl Koopman, and Bryan Patterson, who read (but did not necessarily fully approve) drafts of the manuscript; Barbara Lawrence, who granted access to the large collection of capromyids in the Museum of Comparative Zoology; James Gavan of the University of Florida Health Center, who provided the X-rays on which figure 1 is based; Sue Hirschfeld who prepared figure 1 and plate 1; the National Science Foundation, which financed these illustrations through NSF GB 178; and Lawrence B. Isham who prepared figure 2. Much of this work was done while the author held the position of assistant curator in the Florida State Museum, University of Florida.

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<sup>6</sup>This age seems inordinately early on the basis of the evidence presented by Wood and Patterson (p. 301). If  $P_4$  was nonfunctional in echimyids after Deseadan time, it seems developmentally improbable that a cryptic  $P_4$  crown (a structure elaborated late in ontogeny) would continue to be produced in a Santacrucian form.

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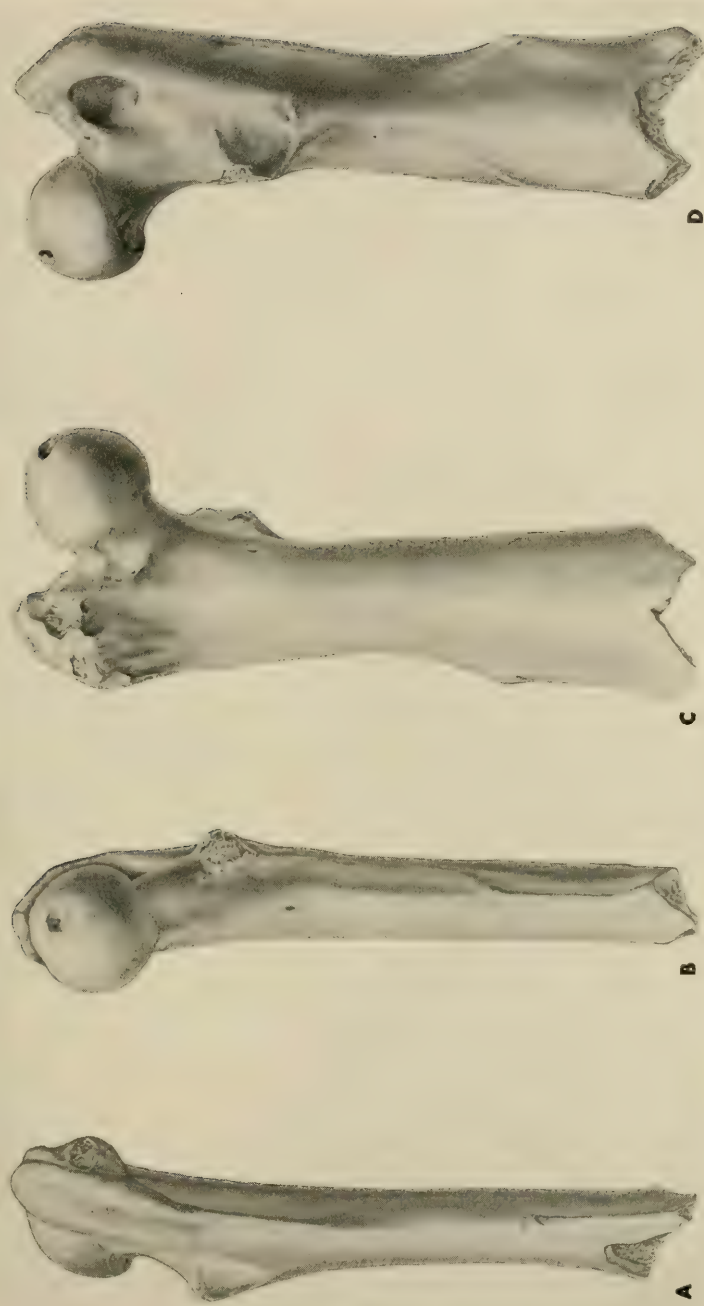
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Fragmentary right femur, U.S.N.M. 253176, of *Quemisia gracilis* in (A) lateral, (B) medial, (C) anterior, and (D) posterior aspect.  
 $1\frac{1}{2} \times$  natural size.









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AN ENDOCRANIAL CAST OF THE  
BRIDGER MIDDLE EOCENE PRIMATE,  
*SMILODECTES GRACILIS*<sup>1</sup>

By C. LEWIS GAZIN

Curator, Division of Vertebrate Paleontology  
United States National Museum  
Smithsonian Institution

(WITH 2 PLATES)

INTRODUCTION

INCLUDED AMONG the materials collected during the 1959 field season in the Bridger Basin of southwest Wyoming is the cranial portion of a skull belonging to the small notharctid primate, *Smilodectes gracilis* (Marsh). Disappointment in not finding the remaining rostral portion was short-lived upon realizing that a suitable, undistorted specimen was now available that could be spared for bone destruction in order to reveal a natural cast of the endocranium, sometimes referred to as a "fossil brain."

The specimen was discovered by my wife, Elisabeth, while collecting with Franklin Pearce and me in an area of badlands between Summer's Dry Creek and Little Dry Creek to the north of Cedar Mountain. The locality is in or near section 29, T. 16 N., R. 110 W., and in beds beneath a thin but conspicuous and widespread sugar-white layer well down in Bridger "B." It has received the U. S. National Museum catalog No. 23276.

Identity of the specimen was readily established by comparison with nearly complete skulls of the species in the collections of the U. S. National Museum. Relevant diagnostic features, particularly in the basicranium of these skulls, were discussed by me in 1958 and illustrations of the better material were included in plates 1-3 of that paper. The synonymy for *Smilodectes gracilis* is there listed, and included is the name *Aphanolemur gibbosus* Granger & Gregory.

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<sup>1</sup> Study of early Tertiary mammals is currently aided by a grant from the National Science Foundation.



The natural cast was developed through flaking off of pieces of bone by careful use of needle and dental tools. This was made possible by the fineness and induration of the internal matrix which revealed a cleavage at contact with the endocranial surface. While essentially all of the dorsal portion and left side of the cast was exposed in this way, the bone on the right side in the ear region was preserved in place for reference purposes. For the latter use, moreover, it was found possible to reassemble portions of the parietal and supraoccipital material removed. Fortunately, an appreciable part of the left temporal area was removed intact without damage to the cast. The only portion of the cast missing is the anterior segment representing the olfactory lobes, presumably included with the unrecovered rostral portion, so that the cast is complete only to the olfactory roots or peduncles.

Information on endocranial casts of fossil primates from the Tertiary of North America is extremely meager. Cope early (1884, p. 246) reported exposure of the natural cast of the left cerebral hemisphere in the skull of *Tetonius homunculus*, stating that he was leaving further examination of it for a future time. So far as I am aware, however, he made no further study of it, although in the following year (1885) he noted a resemblance in the size of the brain and hemispheres to those of *Tarsius*. In 1959 Le Gros Clark also commented on the *Tarsius*-like appearance of the cast. A partially exposed natural cast of *Notharctus "tyrannus,"* together with certain details of brain cavity in other notharctid specimens, was reported by Gregory (1920). His description of this material, including comparison with *Adapis parisiensis*, is rather brief and only the *Adapis* endocranial cast is figured (after Neumayer). Most recently, at the 1964 annual meeting of the Society of Vertebrate Paleontology, Dr. John A. Wilson reported on the discovery of a remarkably good primate skull from the early Tertiary of Texas, which has exposed part of the dorsal surface of the endocranial cast. Further information on this interesting specimen is anxiously awaited.

The pencil-shaded drawings of the *Smilodectes gracilis* endocranial casts included with this report were prepared by Lawrence B. Isham, scientific illustrator for the Department of Paleobiology of the U. S. National Museum. I am indebted to Dr. Tilly Edinger for suggestions and information on undescribed related materials, and to Dr. Malcolm C. McKenna for having the plaster cap removed from the *Notharctus* endocranial cast.

## DESCRIPTION OF THE ENDOCRANIAL CAST

The *Smilodectes* endocranial cast is short and relatively very broad, but no doubt the most striking feature is the remarkable development indicated for the cerebral cortex or neopallium, relatively greater than in any other middle Eocene mammal for which such information is available. Its surface extent, allowing for marked differences in proportions, is nearly comparable to that in the modern lemurs and the lateral extent is entirely comparable, exclusive of folding in such forms as *Lemur*. Except possibly for a very narrow band adjacent to the anterior poles of the mantle, the rhinencephalon would not be visible dorsally. The temporal lobe of the neopallium extended so far ventrally that in lateral view only the tip of the pyriform lobe would be visible. The posterior poles extended well over the mesencephalon, nearly or quite to the cerebellar portion, but as in *Lemur* the vermis and lateral lobes were not overlapped by the cerebrum. The vermis and lateral lobes of the cerebellar portion of the brain were prominently developed, but the cerebellum in general was short and relatively narrow in comparison with the cerebral width.

*Cerebral portion.*—Concerning ourselves for the most part with such details of the neocortical surface that can be inferred from the cast, it is observed that the position indicated for the rhinal fissure is very low on the side of the specimen. Posteriorly it would apparently correspond with the depression occupied by representation of a vascular sinus that extended forward through the cranio-orbital foramen into the orbital fossa (Gazin, 1958, p. 37), much as seen in endocasts of modern *Lemur*. Somewhat forward the fissura rhinalis would apparently rise above the level of the vascular sinus, extending anteromedially, then outward and dorsally as well as forward. At this point it should be noted that there is little or no evidence of a sylvian or pseudosylvian fissure, so that about even with the vallecule sylvii the rhinal fissure, lacking this flexure, turned decidedly outward and upward toward the dorsal surface, rather than more forward as in modern forms. This abrupt rise is, of course, correlated with the shortness of the forebrain. The anterior margin of the neopallium on the dorsal surface is indistinctly shown on the cast but evidently the frontal lobes extended forward nearly to the narrowly constricted portion of the olfactory peduncles. Posteriorly there is no evidence of a floccular notch in the neopallium and the posterior or occipital lobes extended essentially or nearly to the lateral lobes of the cerebellum. Between the posterior poles on the cast a "V"-shaped interval anterior to the vermis exposes representation of the longitudinal

sinus, which is much less distinct forward along the midline. Posteriorly it terminates in a small, prominent knob, evidently homologous with the torcular Herophili in man, but lodged in the parietal rather than in the occipital portion of the skull. From here the lateral sinuses are not represented on the cast until their emergence is noted near the anterolateral margin of the lateral cerebellar lobes.

The surface of the cerebral portion of the cast, owing to the nature of the matrix, shows remarkably fine though incomplete detail of the network of meningeal blood vessels in the dura mater. The surface of the neopallium, as interpreted from the surface of the cast, which strictly speaking represents only the surface of the dura mater with its vascular detail, was evidently nearly, but not quite, lissencephalic. A very shallow, broadly concave depression extends along both sides of the midline in a slightly arcuate, medially convex, path from about even with the frontoparietal suture to approximately the posterior lobes. At the anterior extremity the depression becomes appreciably deeper where it is joined by another feeble depression extending posterolaterally, approximately paralleling the anterolateral margin of the hemispheres. It is observed moreover that the two sides are not quite symmetrical with respect to these features, as the longitudinal depression is a little better defined but not so elongate on the left. Also, the anterolateral depression is better defined on the left, appearing somewhat discontinuous on the right. Presumably these are representations of incipient sulci forming in the neopallium, possibly in response to stresses set up in the transversely already widely expanded mantle in accordance with Le Gros Clark's (1945a) concept, although this would be disputed in favor of a more intrinsic explanation by Connolly (1950). The absence of transverse depressions would seem in keeping with the small freedom of expansion still remaining at the anterior and posterior poles, in the phylogenetic development.

Speculation as to the possible homologies of these shallow depressions in terms applicable to the sulci of the neopallium is perhaps unwarranted; nevertheless, one is tempted to suggest possible correlations. There seems some likelihood that the anteroposterior depression near the midline is related to the sulcus lateralis or the intra-parietal, as this is described as one of the more stable and earlier to appear in the various Mammalia. By itself the more anterolateral depression suggests the coronal or rectus, as it appears along this margin in *Lemur*, but its relation to the presumed sulcus lateralis would appear anomalous since they converge forward rather than



approach the alignment seen in modern lemurs. Perhaps a more plausible suggestion would be that the anterolateral depression paralleling the outer margin represents the suprasylvian sulcus, which in the absence of a sylvian or pseudosylvian fissure might be relatively undeflected. In a possibly comparable situation, but in a more complex setting Tilney (1931, fig. 32) has interpreted a pair of forward converging fissures on a oreodon endocast as the lateral and ectosylvian. Nevertheless, reviewing Edinger's (1948) presentation of the endocranial casts of early horses, something of a parallel is exhibited in Oligocene and somewhat later forms with relatively complex patterns wherein the sulcus cruciatus extended anteromedially from the median part of the suprasylvian, but generally, as in *Mesohippus*, the lateralis falls short of a union with it. Early horses, however, reveal such differently proportioned endocasts, indicating relatively elongate forebrains, that comparison here with a much shortened endocast and in an entirely different mammalian line leaves much to be desired.

Implications as to development or progress in the *Smilodectes* brain that are possibly evident from the cast representation of the neopallium seem in part correlated with osteological structures. For example, the strikingly expanded temporal lobes would among other things suggest significant neocortical location of the acoustic centers. The importance of hearing is, of course, clearly indicated in the tympanic portion of the skull. Moreover, early expansion, for middle Eocene time, of the occipital lobes of the mantle well over the mid-brain would seemingly point to increasing relative importance for the cortical area related to vision. The large forward facing orbits, an adaptation to an arboreal habit, testify to the importance of this sense. Other implications of neocortical expansion are, of course, not evident in bone structure, but no doubt dexterity in an arboreal habit is critically involved, although it is understood that correlation is largely a function of the cerebellum.

*Cerebellar portion.*—The cerebellar portion of the *Smilodectes* endocranial cast, as already noted, is anteroposteriorly short and noticeably narrower than the cerebral portion. The vermis cerebelli extended prominently above the general level or surface of the posterior lobes of the cerebrum, somewhat as in *Lemur* but with relatively a little greater development. No fissura prima is evident although such a structure might be suggested by a slight imperfection across the vermis. This is a trace of the parieto-occipital suture which extends laterally on the cast just anterior to the lateral lobes of the cerebellum. There appears to be a slight offset or fracture of the above along this sutural surface. On a second specimen (U.S.N.M.



No. 17997, pl. 2, fig. 1), however, which has preserved little more than the cerebellar portion of the endocast, there is suggestion of a subdued fissura prima, but this may also correspond to the parieto-occipital suture. The cast shows the paramedian fissure to have been very well developed lateral to the vermis and the cerebellar hemispheres are represented prominently displayed but not nearly as elevated as the vermis. They projected very little above the general level of the cerebral hemispheres and were somewhat elongate transversely but with their long axis slightly oblique as seen from above. There is no indication of a parasagittal fissure but the cast surface of the lobes as well as of the vermis shows traces of the vascular network of the dura mater.

*Petrosal fossa.*—Immediately anteroventral to the cerebellar hemisphere, on the surface of the cast formed by the dorsomedial surface of the petrosal, is indicated the root portion of the flocculus of the cerebellum which occupied a deep floccular or subarcuate fossa in the petrosal. Of about the same size, directly below and medial to the indicated flocculus and on the same surface of the petrosal fossa of the cast is the impression of the aperture of the internal auditory meatus. Immediately behind the position of the flocculus and very close to the posterior bulge representing the lateral sinus can be seen a small, flattened projection which corresponds to the slitlike aperture of the aquaeductus vestibuli. Similarly placed with respect to the pedestal representing the internal auditory meatus but somewhat closer to the latter is a moderately large aperture filling which represents the foramen lacerum posterius. Moreover, further preparation of the corresponding bone surface reveals the presence of the aquaeductus cochleae confluent with the cranial aperture of the foramen lacerum posterius. Just posterior and slightly medial to the position of the foramen lacerum posterius the small pyramidal form with its apex directed somewhat forward is the filling of the condylar or hypoglossal foramen.

The surface of the cast formed by the anterior facing surface of the petrosal, which limited posteriorly the lateral portion of the cerebral hemisphere, is very nearly at a 90° angle from the ventrolateral surface formed by the petrosal. The principal structure evident on this surface is the bulge at the ventral margin representing the internal aperture of the foramen ovale which, incidentally, deeply notches the petrosal. Also distinctive is the posterior termination, at the ventrolateral margin of the surface, of the ridge representing the vascular sinus that appears to follow the rhinal fissure. Directly

above the position of the foramen ovale and nearer the acute angle between the faces of the petrosal fossa is a small flattened prominence which is the filling of the hiatus Fallopii through which the superficial petrosal nerve entered the petrosal.

Evidence may be seen on the cast of a part of the vascular system which essentially surrounded the petrosal. Anterolateral to the cerebellar hemisphere the lateral sinus, at the position of emergence represented on the cast, divided and the lateral sinus proper turned posteriorward where it is represented on the cast by a prominent shelf-like ridge extending along the outer margin of the lateral lobes. It then turned downward to the foramen lacerum posterius. The other branch entered directly a foramen, evidently on the suture between the petrosal and parietal, possibly involving the squamosal, the aqueduct of Verga as used by Saban (1963), that extends slightly forward and outward as well as downward, paralleling the lateral margin of the petrosal fossa. Partway down its course, apparently in the petro-squamosal suture, this duct is joined by an adjacent tube that extends ventrally from the parietosquamosal foramen, permitting vascular communication with the temporal fossa. Just above the outlet of this system through the postglenoid foramen, the canal is joined forward from within the cranial cavity by the vascular representation seen on the side of the pyriform lobe of the cast at about the rhinal fissure. The latter vascular sinus, as has been noted, communicated forward through the cranio-orbital foramen with the orbital fossa and is believed to have included the stapedia artery as well as veins.

A conspicuous ridge on the cast extending anteromedially from the position of the foramen lacerum posterius is seen from the bone to occupy a canal along the suture between the basioccipital and petrosal to near the fossa for the hypophysis. This is no doubt the inferior petrosal sinus. A very short distance anteromedially along this ridge of the cast is an indistinct rise which represents an aperture much better observed on the bone. It corresponds to the forward opening of a canal following the suture between the basioccipital and petrosal or bulla (in part). It opens posteriorly adjacent and medial to the foramen lacerum posterius, and anterior or anteromedially adjacent to the condylar foramen (see Gazin, 1958, pl. 3, fig. 2). This is almost surely the foramen "Fx" in Hürzeler's figures of *Necrolemur* (1948, figs. 27 and 28). I suspect that it served to unite a part of the venus system at the inferior petrosal sinus to the sinus of the vertebral column through the condylar foramen and foramen magnum. It corresponds to the larger and more importantly developed canal in

*Lemur* which extends from the inferior petrosal sinus to its posterior opening adjacent and essentially confluent with the condylar foramen. Except for relative proportions, the cranial circulation noted in the vicinity of the petrosal was essentially like that in modern lemurs.

*Ventral surface.*—The shortness of the rhinencephalon and wide spacing of the prominent, ovate pyriform lobes is particularly evident in the ventral view of the cast. The rhinencephalon tapered sharply forward toward the roots of the olfactory lobes that are missing on the cast. It is of interest to note that the diameter of the posterior or basal portion of the olfactory roots, partially represented on the cast, appears relatively unreduced in comparison with many later primates, suggesting retention of the importantly developed sense of smell. A transversely elongate ridge, slightly concave forward and truncated at each end represents the optic chiasma with its pedicles for the optic nerves at the rather widely separated lateral extremities. Its position is near the olfactory roots and about in line with the anterior margins of the pyriform lobes. Widely spaced crests including representation of nerves III to VI (except  $V_3$ ) bound medially the form of the anterior part of the pyriform lobes. These originate just anteromedial to the pedestal representing the foramen ovale and extend forward nearly to the position of the optic nerve, although the crest on the left side of the cast is broken partway back. Separation between the contents of the sphenoidal fissure and foramen rotundum ( $V_2$ ) is not evident in the cast, although these foramina are distinct, opening close together and close to the optic foramen in the orbital fossa of the skull.

In almost the exact center of the ventral surface of the cast representation of the hypophysis or pituitary body, with its midpoint about  $7\frac{1}{2}$  mm. posterior to the anterior margin of the optic chiasma, is seen as a small, ventrally protruding, nearly hemispherical structure. Its posterior margin superiorly is rather sharply deflected and appears slightly "undercut" by bony projections, the posterior clinoid processes of the basisphenoid. Posterior to this there is slight damage to the cast but the superior surface of the basioccipital and basisphenoid posterior to the clinoid plate and between the inferior petrosal sinuses shows no important deviation from a relatively even surface. There is no indication of the pons as a distinct structure other than a gentle longitudinal convexity not separately defined or distinguished from the inferior surface for the medulla oblongata. A small projection on the cast, however, is observed immediately posterolateral to the position of the hypophysis and about at the anterior extremity of



the ridge representing the inferior petrosal sinus. This is believed to represent a part of the internal carotid artery as it entered the cranial cavity. It occurs nearly at the anterior extremity of the petrosal and is formed by the aperture of a canal that when traced within the bone seems almost certainly continuous with the canal for the arteria promontorii. This branch of the internal carotid was evidently a little larger than in *Lemur* and emerged relatively farther forward, better separated from the hiatus Fallopii.

*Measurements of the Smilodectes endocast.*—The total length of the preserved portion of the endocast (U.S.N.M. No. 23276) is 36 mm. The combined length of the cerebral and cerebellar portions from the anterior margin of the neopallium, so far as can be determined, to the posterior surface of the vermis as represented is about 32.5 mm. The length of the neopallium alone would be about 24 mm. The width of the cast across the temporal lobes of the neopallium, excluding the marginal vascular sinus, is about 29.7 mm., whereas the width of the cerebellar portion excluding the lateral sinus is about 20 mm. The width across the olfactory roots is estimated to be 9 mm. The transverse diameter of the cast representation of the medulla oblongata at the foramen magnum is about 10 mm. It is estimated, from other material of this species that the length of the skull to which this cast belonged was about 68 to 70 mm. from the anterior margin of the premaxillae to the posterior margin of the occipital condyles.

#### COMPARISON OF *SMILODECTES* WITH *NOTHARCTUS* AND *ADAPIS* ENDOCRANIAL CASTS

*Notharctus.*—The most closely related form with which comparison of the endocranial casts might be made is, of course, *Notharctus*, but known comparable material of the latter is rather inadequate. In the principal specimen that Gregory (1920) cited, *Notharctus* "*tyrannus*" (= *N. tenebrosus*), American Museum No. 11478, the endocast is rather poorly delineated. The top of the cast is exposed from near the anterior margin for the frontal lobes to about the top of the vermis posteriorly, and something of the general proportions can be ascertained. The texture of the cast, however, is rather coarse grained so that essentially no detail is evident although as Gregory noted there are "vague indications of the sulcus intraparietalis." There seems, moreover, suggestion of a feeble sulcus (suprasylvian?) parallel to the anterolateral margin, but only on the right side. There is no evidence for a pseudosylvian sulcus, but the lateral margins of the



cast are concealed by the squamosal or are damaged so that its outline can only be approximated; nevertheless, its form was evidently very close to that of *Smilodectes*. Its length seems very nearly the same but its width may be a little less, although there is some distortion evident in the *Notharctus* cast. It cannot, however, be regarded as narrow (see Gregory, 1920, p. 168) in comparison with *Lemur*. The extent of the neopallium was presumably much like that in *Smilodectes*. Representation of the anterior part of the vermis cerebelli is in view and was noted by Gregory to be exposed as in *Lemur*. It is essentially like that in *Smilodectes*. While no mention is made by Gregory of the cerebellar hemispheres, representation of that on the right is faintly discernible, although the one on the left is completely concealed.

The exposed portion of the *Notharctus tenebrosus* endocast is about 30 mm. long by 25 mm. wide. It is estimated, however, that the total length over the cerebral and cerebellar lobes may have been between 32.5 and 35 mm., and the width over the temporal lobes between 27.5 and 30 mm.

Comparison of the *Smilodectes* endocranial cast with endocranial detail reported by Gregory for the fragmentary skull of *Notharctus venticolus* (A.M. No. 14656) could not be made inasmuch as this Wasatchian skull has since been restored for exhibition. The "*N. matthew*" specimen (A.M. No. 13030) cited by Gregory includes a petrosal which contributed to his study. This, however, represents *Smilodectes* and closely resembles the petrosal belonging to U.S. National Museum No. 23276.

*Adapis*.—A comparison of the *Smilodectes* endocast with that described for later Eocene *Adapis parisiensis* was greatly facilitated by Neumayer's excellent appearing figures (1906, pl. 5), reproduced in Gregory's monograph on *Notharctus* (1920, fig. 63), and by the photograph provided by Hofer (1962). From these it is seen that the details of the short and relatively very broad cranial cavity of *Smilodectes* are very unlike those of the *Adapis* specimen, further emphasizing the distinctness of the Notharctidae. However, this is not in agreement with Gregory's unaccountable statement that the endocast of *Notharctus* "is obviously of the same general type, save that in *Adapis* the temporal lobes are more expanded transversely . . ." The cerebral hemispheres of *Smilodectes*, as well as being relatively shorter and broader than in *Adapis*, show evidence of incipient sulci presumed to be lateral and suprasylvian. These are not indicated in Neumayer's figures for *Adapis*, but of more significance, the anterior

and posterior fissura of *Adapis*, which Edinger (1929) has interpreted as the ff. praecentralis inferior and sylvian, were not developed in *Smilodectes*. These greatly affect the outline and form of the *Adapis* endocast. It should be noted, nevertheless, that a small notch far forward on the anterolateral margin of the *Smilodectes* endocast may be in the position of the praecentralis inferior but more probably corresponds to the rhinal fissure.

A particularly striking detail apparent in Neumayer's ventral view of the *Adapis* endocast is the markedly obtuse angle between the faces of the petrosal fossa, with the posterior surface of the temporal lobes facing decidedly outward. In *Smilodectes* this surface is nearly perpendicular to the median vertical plane of the skull. Also noticeable in this view and perhaps better demonstrated in Hofer's photograph (1962, fig. 2c), is the relatively much longer rhinencephalon anterior to the pyriform lobes and much greater separation between the optic chiasma and hypophysis in *Adapis*. Moreover, the pedestals representing the apertures of the floccular fossa and internal auditory meatus are relatively larger in proportion to the size of the cast than in *Smilodectes gracilis* whose brain size is seen to be actually larger than in *Adapis parisiensis*, as determined by the scale of Neumayer's illustrations.

Illustrations by Le Gros Clark (1934, fig. 48; 1945b, fig. 1; and 1959, fig. 121) of an endocranial cast in the British Museum, evidently of a different individual than that figured by Neumayer, show some detail possibly not evident in the other cast. These include representation in the dorsal view (1945b and 1959) of a lateral sulcus as well as of the pseudosylvian, and possibly better development of the anterior lobes of the neopallium (1945b). Moreover, the proportions of the cerebellum are more clearly depicted in Le Gros Clark's figures, showing that the cerebellum was relatively more elongate than in *Smilodectes*. The actual size of the British Museum specimen is not evident as the indicated scales for Le Gros Clark's figures are not in agreement.

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## ABBREVIATIONS FOR ILLUSTRATIONS

a.	Broken surface through olfactory roots.
a.p.	Promontory ramus of internal carotid artery.
a.v.	Aquaeductus vestibuli.
b.	Internal cast of tympanic bulla (incomplete).
c.	Vascular canal between cranio-orbital foramen and postglenoid foramen.
c.f.	Contents of condylar foramen (incl. hypoglossal (XII) nerve and veins).
d.	Contents of sphenoidal fissure or foramen lacerum anterius (incl. nerves III, IV, V, and VI, and ophthalmic vein) and foramen rotundum (incl. nerve V <sub>2</sub> ).
e.a.m.	External auditory meatus.
ExO.	Exoccipital.
f.i.c.	Foramen for internal carotid artery.
fl.	Flocculus of cerebellum.
f.l.p.	Contents of foramen lacerum posterius (incl. nerves IX, X, and XI, and internal jugular vein) plus aquaeductus cochleae.
f.m.	Broken surface through medulla oblongata at foramen magnum.
f.o.	Contents of foramen ovale (incl. nerve V <sub>3</sub> ).
f.p.	Fissura prima?
f.rh.	Fissura rhinalis.
f.sty.	Stylomastoid foramen.
h.f.	Greater superficial petrosal nerve at the hiatus Fallopii or canalis facialis.
hy.	Hypophysis.
i.a.m.	Contents of internal auditory meatus (incl. nerves VII and VIII).
i.p.s.	Inferior petrosal sinus.
l.l.	Lateral lobe of cerebellum or cerebellar hemisphere.
lat.s.	Lateral or transverse sinus.
long.s.	Longitudinal or sagittal sinus.
M.	Mastoid portion of periotic.
m.o.	Medulla oblongata.
O.C.	Occipital condyle.
o.ch.	Optic chiasma.
o.f.	Optic nerve (II) at optic foramen.
p.f.	Paramedian fissure.
p.l.	Pyriiform lobe.
p.s.f.	Parietosquamosal foramen.
p.s.s.	Trace of parieto-supraoccipital suture.
Sq.	Squamosal.
s.l.	Sulcus lateralis.
s.s.	Sulcus suprasylvius?
t.h.	Torcular Herophili or confluens sinuum.
Ty.	Tympanic bulla.
v.c.	Vermis cerebelli.
x.	Anterior aperture of canal between inferior petrosal sinus and "Fx" of Hürzeler.

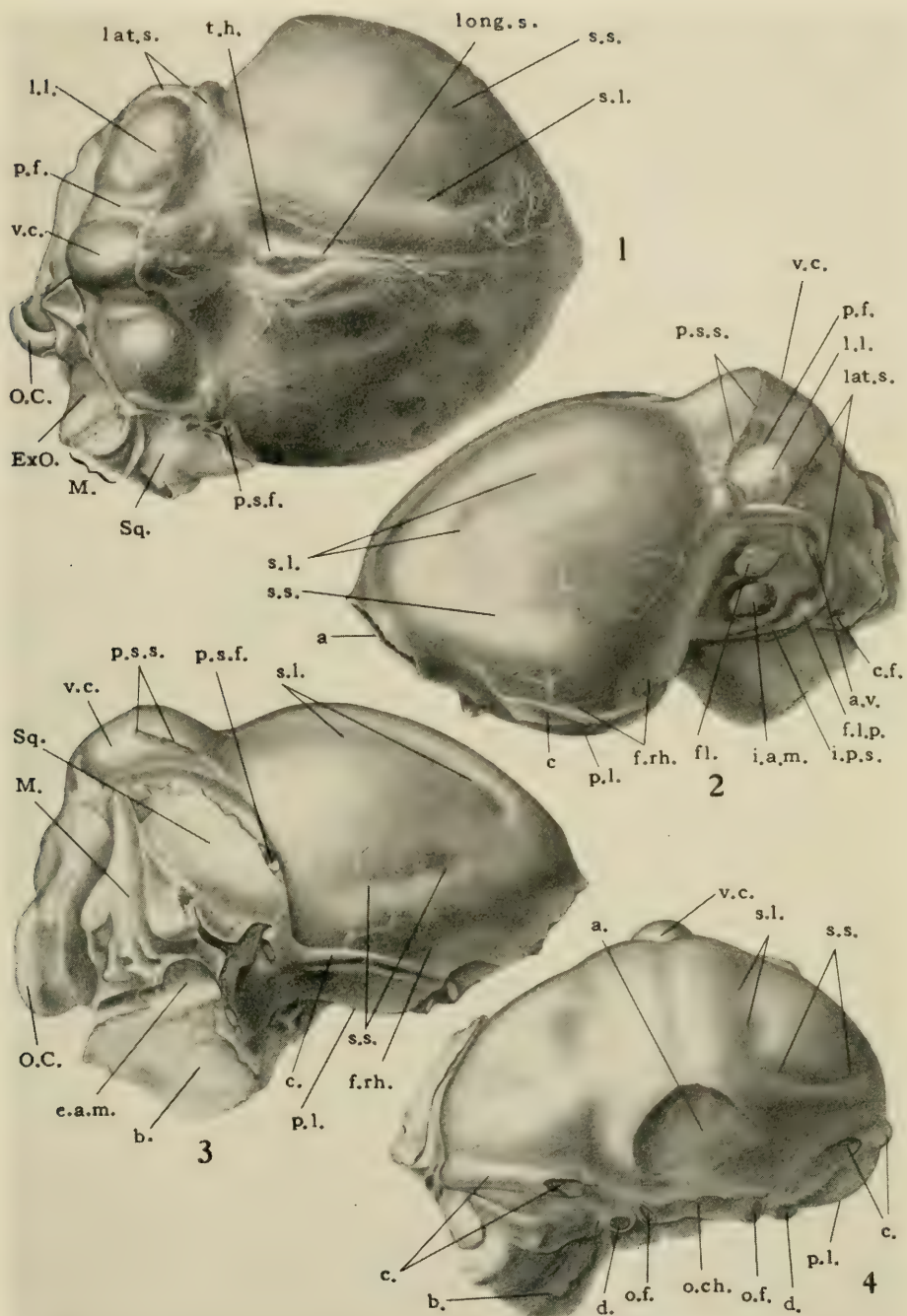
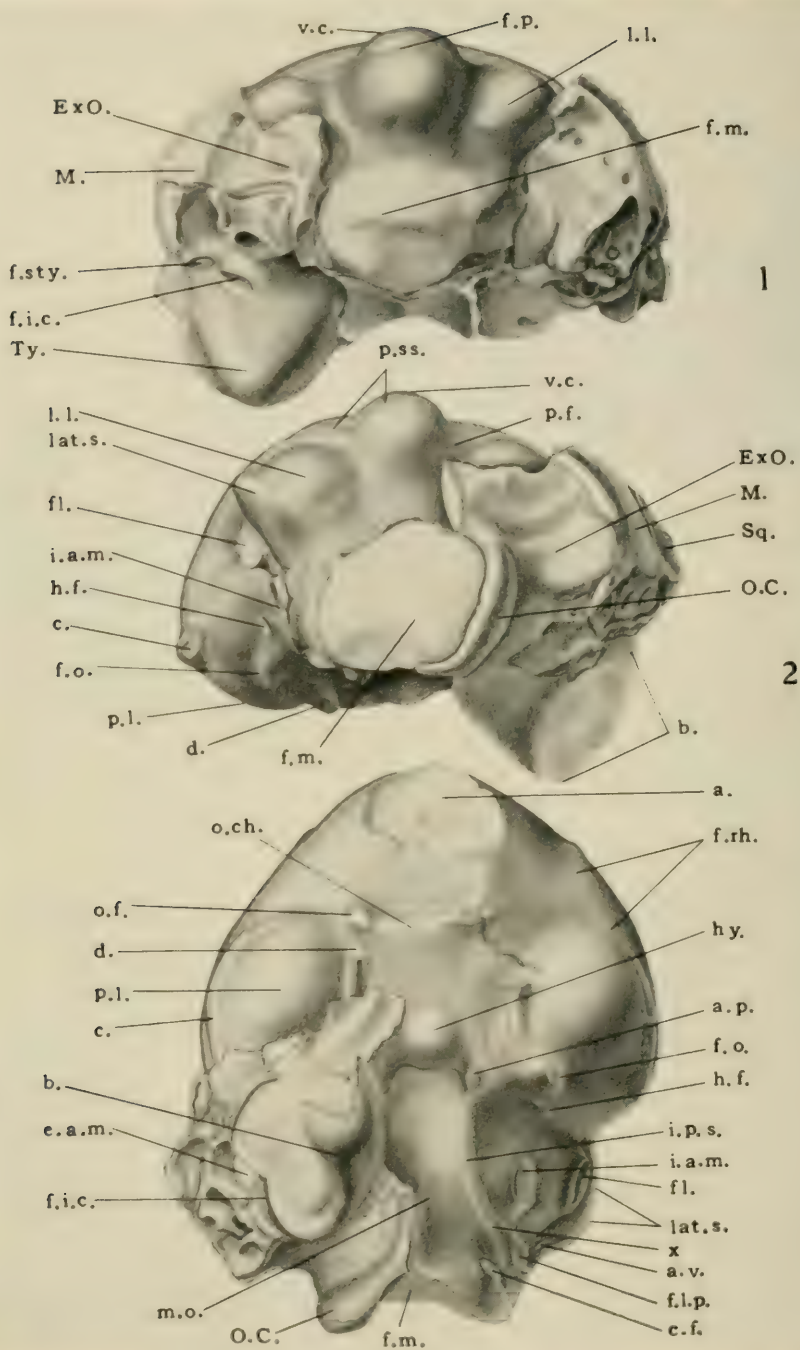


PLATE 1. Endocranial cast of *Smilodectes gracilis*

Figs. 1, 2, 3, 4. *Smilodectes gracilis* (Marsh). Endocranial cast (U.S.N.M. 23276) : 1, dorsal view; 2, lateral view, left side; 3, lateral view, right side; 4, anterior view. Twice natural size. Bridger Basin, Wyoming.

PLATE 2. Endocranial casts of *Smilodectes gracilis*

Figs. 1, 2, 3. *Smilodectes gracilis* (Marsh). Endocranial casts: 1 (U.S.N.M. 17997), posterior view; 2 (U.S.N.M. 23276), posterior view; 3 (U.S.N.M. 23276), ventral view. Twice natural size. Bridger Basin, Wyoming.







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# DISPLAY PATTERNS OF TROPICAL AMERICAN "NINE-PRIMARIED" SONGBIRDS. IV. THE YELLOW-RUMPED TANAGER

By M. MOYNIHAN

*Director, Canal Zone Biological Area  
Smithsonian Institution*

THIS is the fourth in a series of papers on the behavior of some neotropical finches, tanagers, and honeycreepers. It is largely concerned with the behavior of yellow-rumped tanagers observed under natural conditions in the Canal Zone, central Darien, and along the Atlantic coast of the Republic of Panama, between April 1958 and November 1962.

Earlier authors (e.g. Eisenmann, 1955) usually refer to these birds under the name *Ramphocelus icteronotus*. Recently, however, Sibley (1958) has shown that yellow-rumped tanagers interbreed with the birds usually called *R. flammigerus* on the western slopes of the western cordillera of Colombia. He suggests that the two forms are conspecific. If so, yellow-rumped tanagers should be known as *R. flammigerus icteronotus*.

The behavior patterns of yellow-rumped tanagers will be compared with the corresponding patterns of related species described in earlier papers of this series, especially the crimson-backed and silver-billed tanagers, *R. dimidiatus* and *R. carbo* (Moynihan, 1962c), and the brown-capped and sooty-capped bush-tanagers, *Chlorospingus ophthalmicus* and *C. pileatus* (Moynihan, 1962b). All behavioral terms will be used in the same sense as in these earlier papers unless specifically stated otherwise.

Yellow-rumped tanagers are common in many parts of central and eastern Panama. Some aspects of their ecology and general social behavior in this region have already been described in Moynihan, 1962a. Probably the most remarkable feature of their general social behavior is their high degree of intra-specific gregariousness. They are much more gregarious among themselves than are crimson-backed tanagers in the same region. During the nonbreeding season they

are usually found in groups, family parties of four or five individuals and larger flocks of up to ten or twelve individuals. These flocks are very active and mobile but tend to be long-sustained and well-integrated, the members staying close together or coming together repeatedly. Mobile flocks are smaller and less long-sustained on the average during the breeding season, but individuals still follow one another and feed together with some appreciable actual frequency. They also show a definite tendency to form breeding "colonies." Males defend individual territories during the breeding season, but their territories often are small and crowded together in clusters. Even when territories are large, the favorite perches or "stations" of neighboring males may be only a few feet apart. No attempt was made to discover or count nests during the present study, but it was obvious, from the general density of populations, that nests could not be very far apart in many areas (possibly they were less than 50 yards apart in some cases). It is also conceivable that some males are sometimes polygynous. At least several adult males were seen associating with two or more individuals in adult female or juvenal plumage during the first part of the breeding season.<sup>1</sup>

The general social behavior of yellow-rumped tanagers in Panama probably is quite similar to that of the scarlet-rumped or "song" tanagers (*R. passerinii*) of Costa Rica described by Skutch, 1954.<sup>2</sup>

The preflight intention movements of yellow-rumped tanagers, including ritualized Wing-flicking and Tail-flicking, and all their observed unritualized hostile reactions, including both overt attack and escape, seem to be nearly or completely identical in form with the homologous patterns of crimson-backed tanagers (and, probably, all other species of *Ramphocelus*). Yellow-rumped tanagers also perform Gaping, which may be silent or accompanied by Hoarse Notes (see below) and is usually superimposed upon or combined with unritualized aggressive or advance ("pre-attack") movements or intention movements.

As would be expected, in view of their high degree of gregariousness, yellow-rumped tanagers are noisy. Their vocal repertory

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<sup>1</sup> Adult females cannot be distinguished from juvenile birds of both sexes in the field by appearance alone. The individuals referred to as females, without qualification, in the following account were those which performed obviously sexual patterns with adult males.

<sup>2</sup> Yellow-rumped tanagers sometimes occur in mixed flocks with crimson-backed tanagers. This may help to explain certain features of the display behavior of the two species (see page 31).

includes many different kinds of sounds. It is difficult to describe adequately but its principal features may be summarized as follows.

To human ears, three patterns seem to be "extreme" types. These are Nasal Notes, "pure" Rattles, and melodious "Kioo" or "Klloo" Notes.

The ordinary Nasal Notes of yellow-rumped tanagers seem to be very similar to the typical Nasal Notes of crimson-backed tanagers in sound, motivation, and functions. A single Nasal Note might be transcribed by something like "Anh." Notes of this type are uttered by adults of both sexes and by juveniles. They seem to be purely hostile and produced when the tendency to escape is at least slightly stronger than the tendency to attack. They are usually or always alarm or warning signals, but may also serve as contact notes in many circumstances, helping to maintain cohesion among members of the same social group.

The pure Rattles, on the other hand, are very reminiscent of some of the Rattles of *Chlorospingus* species (crimson-backed and silver-billed tanagers seem to have little or nothing in the way of patterns of this type). They are series of very short notes, uttered very rapidly one right after the other. The length of the series is extremely variable. Typical pure Rattles are rather loud, moderately low in pitch, and mechanical or "wooden" sounding. They also are uttered by adults of both sexes and by juveniles and seem to be purely hostile. They are uttered with some appreciable frequency during disputes and fights between individuals of the same sex as well as during a variety of encounters between mates or potential mates. They are obviously aggressive and are usually uttered by attacking birds immediately before or during actual attack, or by birds which are at least advancing toward an opponent (or partner). They are relatively seldom uttered by retreating or escaping birds. They usually, perhaps always, function as threat, probably exclusively so during encounters between individuals of the same sex.

Like the adult males of many other species of tanagers and finches, adult male yellow-rumped tanagers perform "Dawn Calling" during the breeding season. Typical Dawn Calling is a series of notes uttered at approximately regular intervals. The individual notes are of moderate length, and the intervals between notes are usually at least as long as the notes themselves. In some cases all the notes of a series are essentially identical; in others a series will include several different kinds of notes which are not identical but are very similar to one another. Many Dawn Calling performances of some species



consist of two kinds of slightly different notes uttered in more or less regular alternation. In all types of Dawn Calling the length of the series of notes seems to be "indeterminate," i.e. not fixed, varying within very wide limits according to circumstances.

Melodious (and usually rather soft) "Kioo" or "Klloo" Notes are the most distinctive and easily recognized of the notes uttered by male yellow-rumped tanagers during typical Dawn Calling. In these circumstances they may be repeated by themselves alone or (more frequently) uttered in alternation with "Hoarse Flourishes" (see below). They are very similar in sound to, and presumably strictly homologous with, the typical Dawn Calling Notes of crimson-backed tanagers. They seem to be produced by thwarting of some sexual tendency, when overt expression of the tendency by sexual movements is frustrated by the absence of a suitable "object" or partner. They are apparently never closely associated with overt hostility. They are uttered only by males which have become temporarily separated from, or have lost, their mates. Series of such notes seem to be uttered only during the first few minutes of daylight, when almost all sexual activities are most vigorous, and seem to be confined to the height of the breeding season, i.e. the phase of the breeding cycle in which copulations are most frequent. This would suggest that they are very high intensity patterns. The sexual tendencies involved may be pairing and/or copulatory. (Notes of this type are not usually uttered *immediately* before copulation attempts (see below) but this does not necessarily preclude the possibility that birds uttering such notes have activated copulatory tendencies.) Very occasionally isolated adult males will utter the same or very similar notes singly during later periods of the day at the height of the breeding season. There is no reason to suppose that these single notes are not produced by the same type of motivation as the series during Dawn Calling. These single notes are very reminiscent of the "Plaintive Notes" of some other species of tanagers and finches. It is possible, therefore, that the "Kioo" or "Klloo" patterns of yellow-rumped tanagers are also largely or completely homologous with the Plaintive Notes of such species as the brown-capped bush-tanager and the green-backed sparrow, *Arremonops conirostris*.<sup>3</sup> All or most of them probably function to attract females.

Yellow-rumped tanagers seem to utter Nasal Notes about as frequently as crimson-backed tanagers do in similar circumstances. They

<sup>3</sup> All references to the green-backed sparrow throughout this paper are based upon Moynihan, 1963.

utter pure Rattles much less frequently than Nasal Notes. And their "Kioo" or "Klioo" Notes are relatively much less common than the most similar sounding notes of crimson-backed tanagers. All three extreme types of notes, as a group, are uttered much less frequently than a great variety of other notes which sound, to human ears, more or less intermediate between the extremes.

There does in fact seem to be almost complete morphological intergradation between the extremes. Almost every conceivable morphologically intermediate note is uttered at least occasionally, and some intermediates are very common indeed. The latter may be considered "nodal points" in the continuum connecting the extremes.

It will be convenient to give special names to some of the intermediates. Among these are Hoarse Notes, "Greeting" Notes, "Tzzheet" Notes, Hoarse Flourishes, and Thin Rattles.

The Hoarse Notes of yellow-rumped tanagers are harsh rasping sounds of more or less moderate length uttered singly or in short series of two or three notes one right after the other. Most notes of this type could be transcribed by something like "Zraa" or "Zraanh" or "Sraah." When uttered in series the successive notes usually are very similar to one another. They all sound very much like some of the Hoarse Notes of such related species as the crimson-backed tanager and the green-backed sparrow. In the latter species Hoarse Notes are easily recognized as qualitatively distinct from all other vocal patterns. This is not true of the Hoarse Notes of yellow-rumped tanagers. They usually or always have a slight trace of a rattling quality or "undertone." As a result they sound more or less perfectly intermediate between typical Nasal Notes and pure Rattles. They certainly intergrade with both.

The Hoarse Notes of yellow-rumped tanagers are not only less distinct than those of crimson-backed tanagers and green-backed sparrows but also much less common. This seems to be due to the fact that yellow-rumped tanagers utter pure Rattles and Thin Rattles in many of the social situations in which the latter species utters one or more types of Hoarse Notes. Yellow-rumped tanagers seem to utter Hoarse Notes with appreciable frequency in only two situations. An individual caught by a predator (e.g. a human being) utters loud and long Hoarse Notes (often relatively high pitched and urgent sounding). These notes seem to be essentially similar to the patterns of crimson-backed tanagers which have been called "Hoarse Screams." Like the latter they seem to be purely hostile and high intensity, produced by strong activation of both attack and escape

tendencies. The two tendencies are probably more nearly equal in strength during Hoarse Screams than during either Nasal Notes or pure Rattles. Softer and shorter Hoarse Notes are uttered during intraspecific encounters. In the course of the present investigation they were heard most frequently during encounters between adult males and (known or presumed) females. They were uttered by males approaching or being approached by females, usually or always when the males were not very familiar with and/or obviously hostile toward the females. Some of these notes were combined with Gaping or actual attack movements. Similar notes certainly are uttered by both adult females and juveniles, although more rarely, in some hostile or partly hostile circumstances; but I cannot say very much about them, primarily because they are so soft that I may have missed many of them in the field. All these comparatively soft Hoarse Notes must be purely hostile or produced by simultaneous activation of both hostile and sexual tendencies. They probably are produced when the attack and escape tendencies are nearly equal to one another but weaker than when loud Hoarse Notes are uttered. If a sexual tendency is also involved, it is almost certainly relatively weak.

Adult males may utter slightly different "Greeting" Notes when joining or being joined by females with whom they are on fairly good terms. In their most typical form these notes are slightly hoarse in quality, but less so than the typical Hoarse Notes described above, and without any rattling undertone. They are very soft and apparently always uttered in series. Typical series might be transcribed as "Tsee-whee-hee" or "Zhee-wee-tsee-tseewee" or "Zee-a-waa-zaa-waa." All these patterns sound intermediate between typical Hoarse Notes on the one hand and Hoarse Flourishes and/or "Tzzheet" Notes on the other hand. They certainly intergrade with the former and probably with the latter. The only birds heard to utter typical "Greeting" Notes were captive individuals kept in aviaries on Barro Colorado Island; but the notes are so soft that one would not expect a human observer to be able to hear them in the field. They probably are produced by the same hostile motivation as typical soft Hoarse Notes, with an added (or stronger) sexual component. The possession of a special "Greeting" pattern, obviously related to Hoarse Notes but apparently uttered only during encounters between males and females of the same species, may be another special resemblance between yellow-rumped tanagers and brown-capped bush-tanagers.

Among the most common vocal patterns of yellow-rumped tanagers are short, monosyllabic, rather high pitched and hard sounding notes



which might be transcribed as "Tzzheet." These notes are uttered by adults of both sexes and by juveniles, most frequently by adult males. With very few exceptions they are uttered only by individuals who are isolated or alone, i.e. who have become separated (by a distance of at least several meters) from their mates or other members of their own social group. Unlike the melodious "Kioo" or "Klioo" Notes they are uttered quite frequently at all times of the year and during all periods of the day.

There are many resemblances between these notes and the vocalizations of crimson-backed tanagers which were called "Plaintive Notes" in Moynihan, 1962c. The two patterns certainly are nearly identical in sound, especially when heard at a slight distance. In an earlier paper (Moynihan, 1962a), both were transcribed as "Tseet." Subsequent and closer observations, however, have revealed that the "Tzzheet" Notes of yellow-rumped tanagers are usually slightly harder and hoarser, with a more pronounced "buzzy" quality, than the corresponding notes of crimson-backed tanagers. They are, in other words, slightly more similar to typical Hoarse Notes in tone.<sup>4</sup>

It has been suggested that "Tseet" Notes are produced by thwarting of some gregarious motivation as well as several different types of "friendly" motivation, including pairing and parental tendencies. This may well be true of some or all "Tzzheet" Notes also, as they seem to occur in almost exactly the same range of circumstances. Both patterns may function as "summons," a means of calling in or attracting mates and other members of the family or social group. All these resemblances would indicate that the two patterns must be closely related phylogenetically.

"Tzzheet" Notes seem to be uttered more frequently on the average than the corresponding notes of crimson-backed tanagers in similar situations. They must have a comparatively low releasing threshold. They also are uttered in series more frequently than are "Tseet" Notes, and many series of "Tzzheets" are much longer than any series of "Tseets." Adult male yellow-rumped tanagers sometimes utter long series of "Tzzheet" Notes at very regular intervals of approximately the same length as the intervals separating "Kioo" and

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<sup>4</sup> The term "Plaintive" is not particularly suitable as a name for the crimson-backed tanager notes. It was applied to them only because they were thought to be strictly homologous with the Plaintive notes of other species. This may or may not be correct (see page 8). In order to avoid confusion these crimson-backed tanager patterns will be called simply "Tseet" Notes throughout the following discussion.



"Klloo" Notes during the Dawn Calling described above. They may utter such series at any time during the day, including the first half hour of daylight. Series of "Tzzheet" Notes at dawn are relatively most common early in the breeding season, before copulations have become frequent, and are relatively rare at the height of the breeding season, when "Kloo" or "Klloo" Dawn Calling is most common. If both performances are produced by thwarting of the same type of sexual motivation, it is probably weaker when the "Tzzheet" series are uttered than when the "Kloo" series are.

There are certain connections between "Tzzheet" Notes and unmistakably hostile patterns. Typical "Tzzheet" Notes intergrade with typical Hoarse Notes. They also are associated and intergrade with the partly hostile Thin Rattles relatively frequently (see page 9). Occasionally they are uttered immediately before or after actual fights and/or are accompanied by hostile Back-ruffling (see page 13). It is possible, therefore, that at least some "Tzzheet" Notes include a hostile component. If so the hostile component probably is relatively weaker than in the "Greeting" Notes.<sup>5</sup>

A variety of vocal patterns may be grouped together under the name of "Hoarse Flourishes." All are bisyllabic notes. They can be transcribed in many slightly different ways, e.g. "Tseeeee-up," "Wheeeee-ah," "Tseeeee-yah," "Tseeyoo," "Eeyah," "Kheezaa," and "Kheezoo." All notes of this type sound like bisyllabic versions of typical "Tzzheet" Notes. The first syllable is always similar to a "Tzzheet" Note in pitch, and the second syllable is apparently always at least slightly lower in pitch. Both syllables are slightly hoarse in the same way as "Tzzheet" Notes. These Hoarse Flourishes

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<sup>5</sup> "Tzzheet" Notes are almost as similar to the typical Plaintive Notes of such species as the brown-capped bush-tanager and the green-backed sparrow as to the "Tseet" Notes of crimson-backed tanagers. They resemble those Plaintive Notes in some aspects of form, i.e. the fact that they include a fairly clear "eee" sound and are less harsh or rasping than many other vocal patterns of the species, as well as in their largely or completely nonhostile motivation and their function as "summons." If they do not include a hostile component they may be completely homologous with typical Plaintive Notes. If they are partly hostile they may be partly homologous, i.e. their basic form may be homologous with the Plaintive Notes of other species but their hoarse quality may have been derived from another source. In either case they are probably related to the "Kloo" or "Klloo" Notes (see also page 21).

The comparative position of the "Tseet" Notes of the crimson-backed tanager is somewhat obscure. They are less hoarse than "Tzzheet" Notes but hoarser than the Plaintive Notes of the brown-capped bush-tanager or the Green-backed sparrow. If the "Tzzheet" Notes are of compound origin it is possible that the "Tseet" Notes are also.

may be uttered by themselves alone or in a variety of obviously unritualized associations with many other vocal patterns, or in a close and apparently ritualized association with typical "Tzzheet" Notes and Thin Rattles. The latter performances seem to be something of a special case, and will be discussed separately below. The other Hoarse Flourishes are uttered almost exclusively by adult males and are particularly characteristic of the height of the breeding season. They are uttered in much the same way and in much the same circumstances as melodious "Kioo" or "Klioo" Notes. They are almost always uttered by isolated birds, singly, at any time of the day or in Dawn Calling series. They are, in fact, the most common of the Dawn Calling notes at the height of the breeding season, much more common than "Kioo" or "Klioo" Notes. Many Dawn Calling performances are composed of Hoarse Flourishes alone. Less frequently Hoarse Flourishes and "Kioo" or "Klioo" Notes are uttered in regular alternation. Typical Hoarse Flourishes intergrade with both typical "Tzzheet" Notes and typical "Kioo" or "Klioo" Notes. All this would suggest that Hoarse Flourishes are really intermediate between "Tzzheet" Notes and "Kioo" or "Klioo" Notes, produced by intermediate motivation. They certainly function as another summons to call in or attract mates.<sup>6</sup>

Thin Rattles are uttered by adult yellow-rumped tanagers of both sexes and by juveniles. A typical Thin Rattle sounds very much like a pure Rattle but is higher-pitched on the average and "thinner" in sound, less penetrating but not necessarily softer. Some Thin Rattles seem to remain at the same pitch throughout. In others the pitch declines gradually and continuously but only slightly. They all sound perfectly intermediate between typical pure Rattles and typical "Tzzheet" Notes, like more or less prolonged "Tzzheet" Notes which have broken up or like pure Rattles which have been transposed into a higher key. They also intergrade with both "Tzzheet" Notes and pure Rattles. They are frequently associated with both overt hostility, especially aggression, during disputes between individuals of the same as well as opposite sex, and with a variety of

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<sup>6</sup> The Hoarse Flourishes of yellow-rumped tanagers are somewhat similar to the Flourishes of *Chlorospingus* spp. in form, motivation, and function. They may be completely homologous with the latter. If, however, their hoarse quality is an indication that an hostile component is involved, then the homology probably is only partial. In any case, the relationship between the Hoarse Flourishes of yellow-rumped tanagers and the Flourishes of *Chlorospingus* spp. probably is exactly the same as the relationship between the "Tzzheet" Notes and the Plaintive Notes of the same species.



patterns containing obvious sexual elements during encounters between mates or potential mates. It seems likely, therefore, that they are produced by motivation which is intermediate between that of typical pure Rattles and that of typical "Tzzheet" Notes, i.e. when both hostile tendencies are activated, and the attack tendency is relatively much stronger than the escape tendency, but some non-hostile "friendly" tendency (or tendencies) is activated simultaneously. All or most Thin Rattles by themselves probably function as threat.

By themselves, however, they are relatively rare. They usually are uttered in very close temporal association with "Tzzheet" Notes and Hoarse Flourishes. This association is quite stereotyped in some ways and would appear to have become ritualized as a whole. A typical complete performance consists of one "Tzzheet" Note followed immediately by one Thin Rattle followed immediately by one Hoarse Flourish. The sequential relations appear to be almost invariable. Sometimes one of the three patterns may be omitted, but the remaining two apparently always occur in the same sequence as in typical complete performances. Thus, for instance, one may hear incomplete performances which consist of one "Tzzheet" Note followed by one Thin Rattle, or one "Tzzheet" Note followed by one Hoarse Flourish, or one Thin Rattle followed by one Hoarse Flourish, but not one Thin Rattle followed by one "Tzzheet" Note or one Hoarse Flourish followed by one "Tzzheet" Note. The nearest thing to a reversal of sequence occurs during some complex performances which consist of one "Tzzheet" Note, followed by one Thin Rattle, followed by one Hoarse Flourish, followed by a second Thin Rattle, followed by a second Hoarse Flourish; but these performances obviously are nothing more than two typical complete sequences uttered so rapidly that they are partly "telescoped" together. The length of the Thin Rattle in both complete and incomplete performances is extremely variable. Most of the terminal Hoarse Flourishes are short and rather "slurred," much shorter than many of the Hoarse Flourishes uttered singly or in Dawn Calling series. Almost all the Hoarse Flourishes associated with "Tzzheet" Notes and Thin Rattles are of the type which can be transcribed as "Eeyah."<sup>7</sup>

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<sup>7</sup> The complex "Tzzheet" Note—Thin Rattle—Hoarse Flourish performances, considered as a unit, seem to intergrade with both series of "Tzzheet" Notes and single Hoarse Flourishes. Intermediates may take such forms as a series of two or three "Tzzheet" Notes uttered more rapidly than usual and followed by a single brief note of slightly lower pitch (i.e. a trace of the second syllable of Hoarse Flourishes) or of an unusually prolonged Hoarse Flourish which includes a trace of rattle "undertone" toward the end of the first syllable. (These

If the individual patterns retain the same functions when they are uttered together as when they are uttered separately (and my observations would suggest that they do), then the "Tzzheet"—Thin Rattle—Hoarse Flourish performances probably function as "song," as the term is used in this series of papers. When uttered by a bird of one sex they may attract birds of the opposite sex and repel other birds of the same sex.

Adult male yellow-rumped tanagers frequently interrupt their Dawn Calling to utter purely or predominantly hostile notes. Such ambivalent performances may subserve the same functions as stereotyped "Tzzheet"—Thin Rattle—Hoarse Flourish patterns, but they are extremely variable in form and do not seem to be ritualized per se. Yellow-rumped tanagers apparently do not utter stereotyped series of Nasal Notes and "Tzzheet" Notes (or any other primarily sexual pattern) in regular alternation like the series of Nasal Notes and "Tseet" Notes uttered by adult male crimson-backed tanagers.

The "Tzzheet" Note—Thin Rattle—Hoarse Flourish complex, as a whole, is remarkably similar to the equally stereotyped Rattle—Flourish performances of brown-capped bush-tanagers. The rattling and Flourish parts of the sequences of the two species certainly are at least partly homologous. The Rattle—Flourishes of brown-capped bush-tanagers are often preceded by "Tsit" Notes. These "Tsit" Notes, when uttered by themselves alone, do not appear to be as strongly sexual as the "Tzzheet" Notes of yellow-rumped tanagers, but their association with Rattle—Flourishes would suggest that they may be phylogenetically related to "Tzzheet" Notes (and the Plaintive Notes of other species). This suggestion may be supported by the fact that sooty-capped bush-tanagers utter similar sounding "Tsit" Notes to call in or attract mates.

Yellow-rumped tanagers also utter rattling sounds which are very much softer than either typical pure Rattles or typical Thin Rattles. These may be called Muffled Rattles. They are rarer than the other kinds of Rattles, usually prolonged, and associated with vigorous reactions between individuals in close proximity to one another. They seem to be uttered most frequently by adult males approaching or being approached by adult females or juveniles at the height of the breeding season. Once I heard an adult male utter a Muffled Rattle immediately before an apparently successful copulation. Many similar or identical patterns were uttered during an unusually prolonged and

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latter are also, of course, intermediate between simple Thin Rattles and Hoarse Flourishes.)



violent dispute (including many contact fights) between two adult males at the height of the breeding season. And once I heard a bird in female or juvenal plumage (probably an adult female) utter a single Muffled Rattle immediately before feeding another bird in similar plumage (presumably a juvenile). It is evident that Muffled Rattles are very high intensity patterns. They seem to intergrade with both typical pure Rattles and typical Thin Rattles. Possibly they are somewhat heterogeneous. Some Muffled Rattles may be nothing more than unusually soft pure Rattles, while others may be nothing more than unusually soft Thin Rattles. (All the extreme Muffled Rattles are so soft that I could never tell which of the louder Rattle patterns they most resembled in pitch). If the Muffled Rattles are heterogeneous in this way, then some may be purely hostile, produced when the attack tendency is strongly predominant over the escape tendency but both are stronger than during typical pure Rattles, while others may be partly hostile and partly sexual, produced when the relative strength of the hostile and sexual tendencies is the same as in typical thin Rattles but the actual strength of all the tendencies is greater.

Some or all of the Muffled Rattles of yellow-rumped tanagers may be strictly homologous with the Muffled Rattles which are uttered by male brown-capped bush-tanagers approaching females and immediately before copulations.<sup>8</sup>

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<sup>8</sup> Two other vocal patterns of yellow-rumped tanagers appear to be set somewhat apart from the mass of intergrading patterns described above.

One captive adult male was heard to utter many "Tsit" Notes. They were much softer and shorter than typical "Tzzheet" Notes. They were uttered singly or repeated at irregular intervals (i.e. they were never organized in regular series like Dawn Calling notes). The male uttered these notes after being in captivity, in the same cage, for over a year, whenever he saw a human being in the distance. If the human came closer he usually began to perform escape movements or intention movements and to utter typical Nasal Notes instead of the "Tsits." Thus it would appear that the "Tsit" Notes were low intensity alarm patterns. Presumably they were produced when the escape tendency alone was activated or (more probably) when both hostile tendencies were activated simultaneously and escape was much stronger than attack but both tendencies were weaker than when Nasal Notes are uttered. These "Tsit" Notes were much too weak to be heard in the field. Thus I do not know if they are really typical of the species or not. If so they may be strictly homologous with the soft "Tsip" or "Chik" alarm notes of green-backed sparrows. In any case it seems very unlikely that they are closely related to the louder but otherwise similar sounding "Tsit" notes of either *Chlorospingus* species or some other species of *Ramphocelus* (see pages 30 and 31).

One wild male in typical adult plumage was observed to perform something which looked like "silent song." He sat for several minutes opening and

Figure 1 is an attempt to show the relationships between the more common and easily recognizable vocal patterns of adult male yellow-rumped tanagers in diagrammatic form.

Of all the nonvocal display patterns of yellow-rumped tanagers, perhaps the most interesting and complex are the feather-raising patterns. Yellow-rumped tanagers apparently do not have any general ruffling pattern, involving all the head and body plumage simultaneously, like that of crimson-backed tanagers. Instead they have a variety of patterns of more limited extent. These include Head-ruffling, Head-fluffing, Back-ruffling, and Belly-fluffing. Tail-fanning may be associated with the same group of patterns. It will also be convenient to consider a special form of depression of the feathers, Crown-flattening, in connection with some of the feather-raising patterns.

All these patterns seem to be ritualized. With the exception of Tail-fanning, they seem to be performed only by adult males.

Back-ruffling is a more or less extreme raising of all the yellow feathers of the lower back and rump. The feathers are raised in such a way that their tips are conspicuously separated. The wings usually are drooped (but not spread to any appreciable extent) at the same time. Back-ruffling is a very common pattern. It occurs in a wide variety of social situations, but it seems to be much more closely linked to aggression than to any other kind of overt unritualized activity. It is frequently performed by attacking birds before and/or after delivering attacks. It may be silent or accompanied by vocalizations. By far the most common vocalizations associated with Back-ruffling are rattling patterns, all types of rattling patterns, including "Tzzheet"—Thin Rattle—Hoarse Flourish performances. All this would suggest that Back-ruffling is primarily an expression of the attack tendency. Various kinds of Back-ruffling performances are illustrated in figures 2 to 6 in conjunction with some notes on the circumstances in which they were observed.

Belly-fluffing is a raising of all the feathers of the lower breast and

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closing his bill while his throat went in and out, just as if he were uttering many notes in rapid succession; but I could not hear any sound at all during the performance, even though I was less than five feet away from him at the time. His whole performance was very reminiscent of the initial stage in the development of "Juvenile Subsong" or "Whispering Warbles" in young male crimson-backed tanagers. Most of the other male yellow-rumped tanagers in the same area at this time were molting from juvenal plumage into adult plumage. It is possible that the male which performed "silent song" had just completed the molt into adult plumage and was still behaving as a young bird.

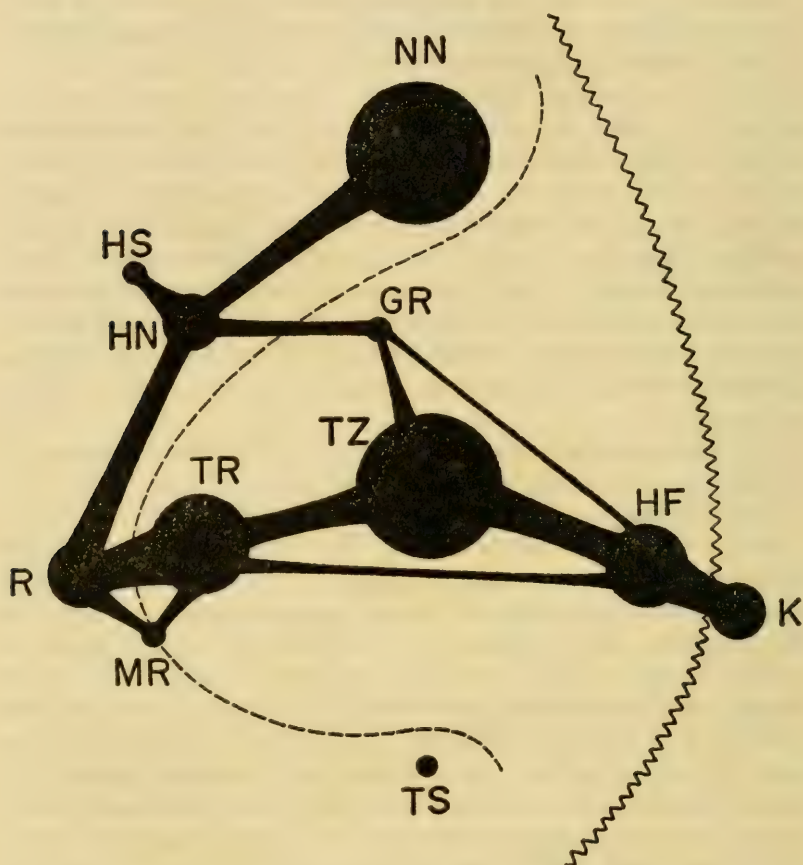


FIG. 1.—Apparent relationship between the most common and/or most easily recognized vocal patterns of adult male yellow-rumped tanagers. (NN=Nasal Notes. HN=relatively soft Hoarse Notes. HS=Hoarse "Screams." GR="Greeting" Notes. R=pure Rattles. TR=Thin Rattles. MR=Muffled Rattles. TZ="Tzzheet" Notes. HF=Hoarse Flourishes. K="Kioo" or "Klioo" Notes. TS=soft "Tsit" Notes.)

The size of the circles representing different types of notes is very roughly proportional to the frequency of the notes. The thickness of the lines connecting the different types of notes is very roughly proportional to the frequency of intermediates between the notes connected.

All the vocal patterns to the left of the zigzag line seem to contain hostile components (i.e. seem to be produced by hostile motivation, alone or in combination with other nonhostile tendencies). All the patterns to the right of the dotted line are frequently or always partly or wholly sexual.



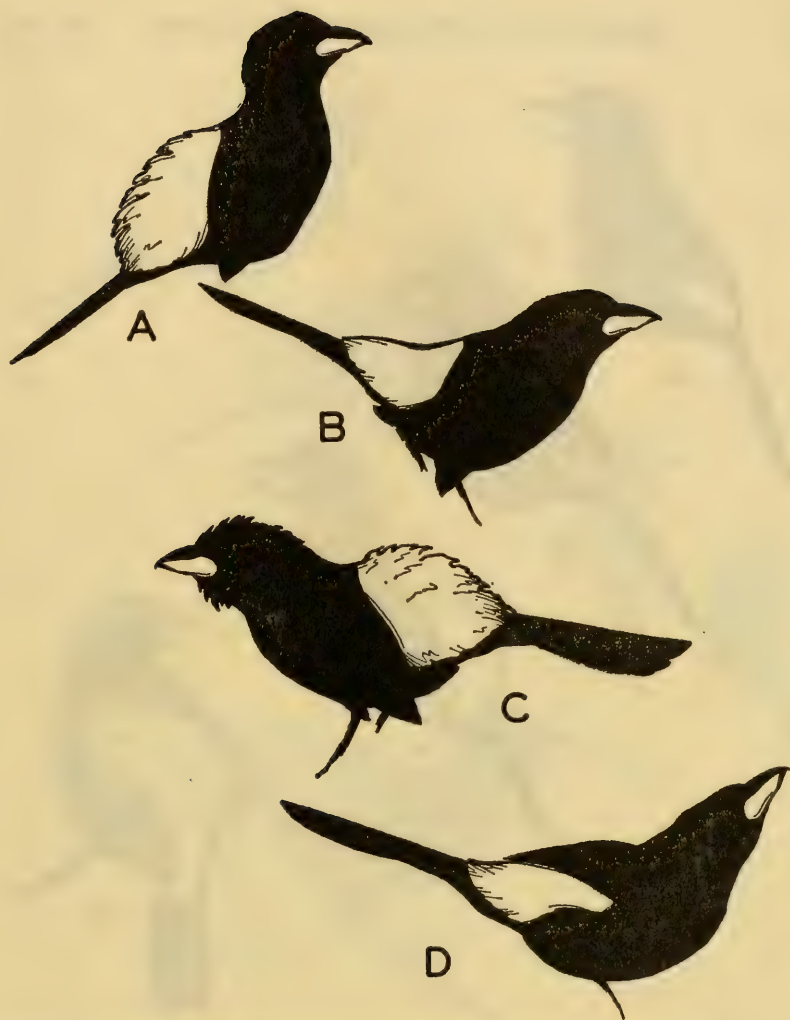


FIG. 2.—Display postures of adult male yellow-rumped tanagers.

From top to bottom:

a. Posture assumed by a male after a dispute with another male. With extreme Back-ruffling. At first the bird in this posture was silent; then it uttered Thin Rattles and/or pure Rattles.

b. Posture of a male immediately after Turning-away from a female at the height of the breeding season. The wings are drooped but there is no Back-ruffling. The bird was silent while it remained in this posture.

c. Posture of another male immediately after Turning-away from a female (with a second male perched near by). With Head-ruffling, Back-ruffling, and Tail-fanning. The Head-ruffling is somewhat anomalous, but closest to the "angular" type. The bird was silent while it remained in this posture.

d. Silent Bill-up Tail-up Posture, with Crown-flattening and asymmetrical positioning of the wings, assumed by a male immediately after an apparently successful copulation. (The tail may have been raised a little higher during part of the time that the male remained in the posture.)



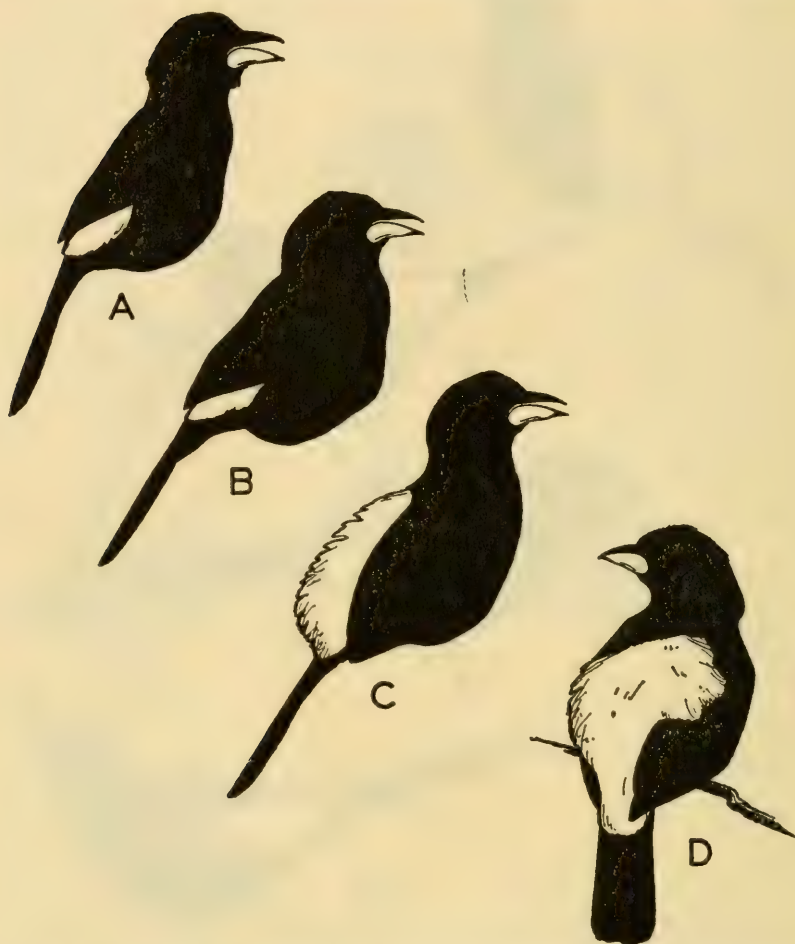


FIG. 3.—Postures accompanying vocal patterns of adult male yellow-rumped tanagers.

From top to bottom:

a. Typical posture accompanying Dawn Calling of Hoarse Flourishes and/or "Kioo" or Klioo" Notes. With typical Head-fluffing.

b. Posture frequently or usually assumed when "Tzzheet" Notes are uttered in series. With some Head-fluffing and Belly-fluffing.

c. Most typical posture accompanying "Tzzheet"—Thin Rattle—Hoarse Flourish performances. With moderate Back-ruffling.

d. Posture assumed by a male uttering a series of "Tzzheet" Notes. This individual looked from side to side between and during the notes. It also performed Back-ruffling. The wings were held in such a way that the yellow area of the lower back and rump appeared to be irregular in shape (this is not uncommon).

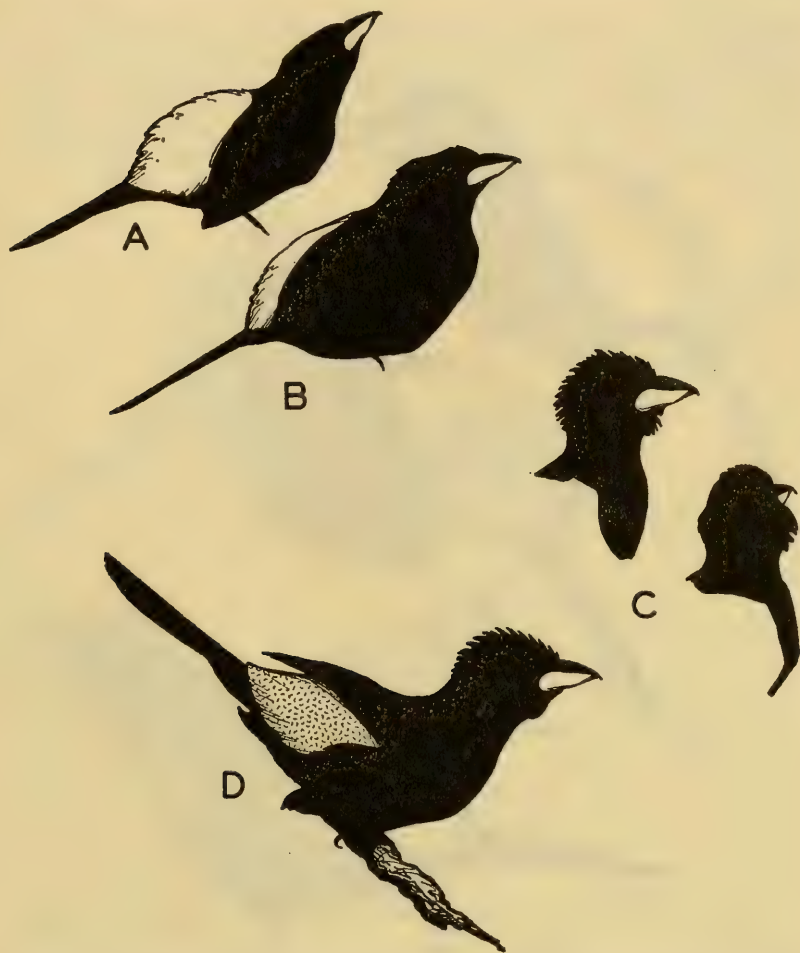


FIG. 4.—Postures of adult male yellow-rumped and orange-rumped tanagers.

From top to bottom:

a. Peculiar posture assumed by a captive male yellow-rumped tanager, kept in an aviary with a female of the same species, during a dispute with another male of the same species introduced into the same aviary. This appeared to be a preflight posture (the upward pointing of the head and bill being an intention movement of flying upward, not an indication of the ritualized Bill-up Tail-up). It was combined with Crown-flattening and extreme Back-ruffling, and accompanied by Thin Rattle—Hoarse Flourish calls.

b. "Fluffed Hunched" posture assumed by the introduced male during the same dispute. With a trace of Crown-flattening, slight Back-ruffling, and extreme Belly-fluffing. Silent.

c. Side and rear views of typical "angular" Head-ruffling by yellow-rumped tanagers.

d. Preflight, crouching, posture of a male orange-rumped tanager, with extreme "rounded" Head-ruffling.

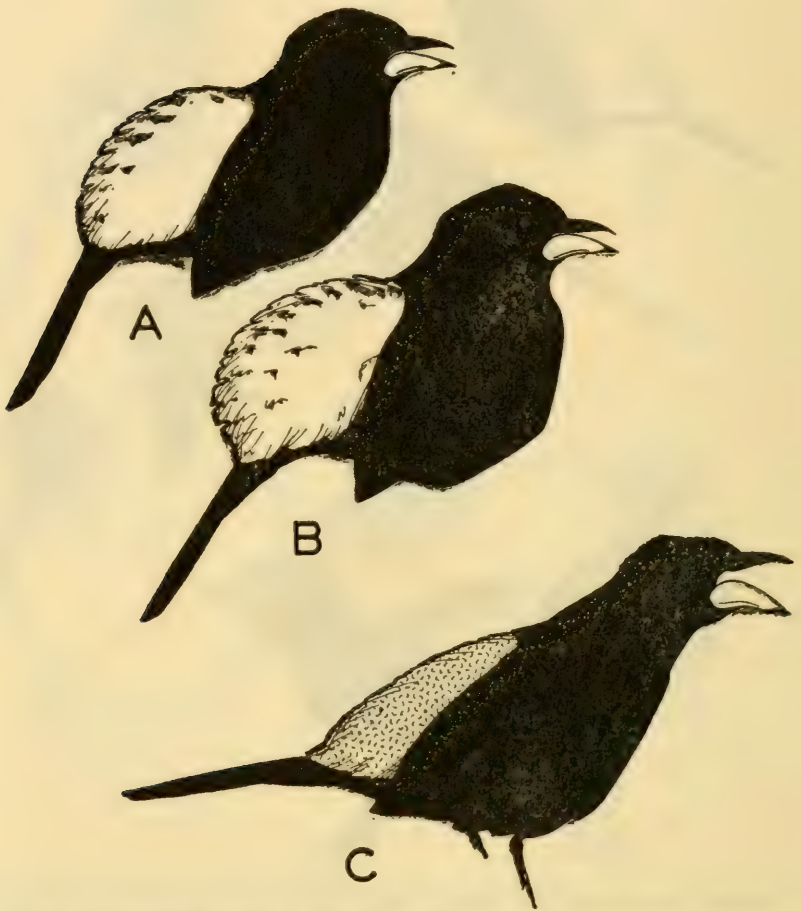


FIG. 5.—Postures of adult male yellow-rumped and orange-rumped tanagers. From top to bottom:

- a. Posture of a male yellow-rumped tanager uttering "Tzzheet"—Thin Rattle—Hoarse Flourish calls while alone. With extreme Back-ruffling, some Crown-flattening, and (perhaps) a trace of Belly-fluffing.
- b. Posture of the same individual uttering Thin Rattles, a few seconds later, after being joined by an adult female or a juvenile.
- c. Posture of a male orange-rumped tanager uttering Rattles while facing a female silver-billed tanager.

belly. This raising may be quite extreme, but the tips of the feathers are seldom or never separated from one another in a conspicuous manner. Belly-fluffing seems to be rarer than Back-ruffling. Birds uttering "Tzzheet" Notes may show a slight to moderate amount of Belly-fluffing (see figure 3b). This is particularly likely to occur when

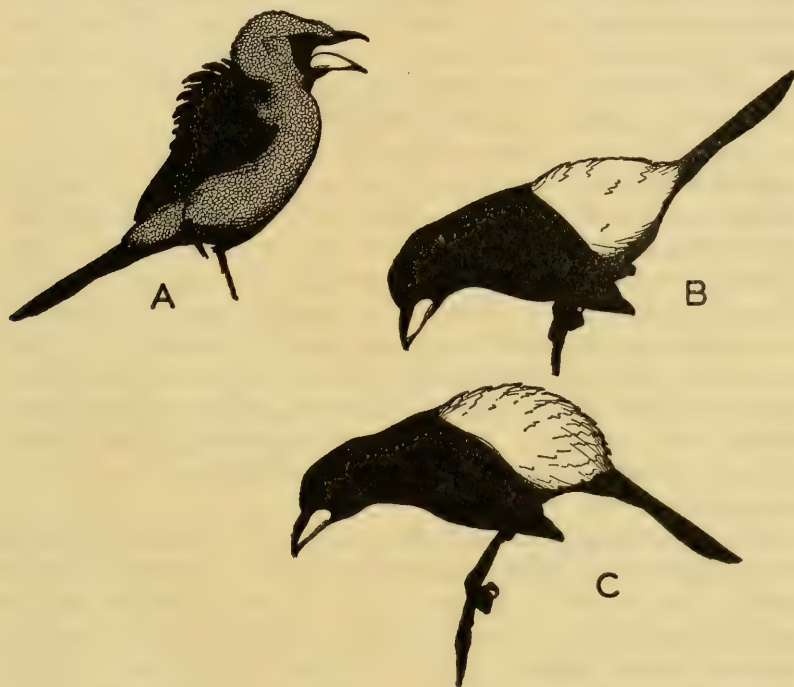


FIG. 6.—Postures of a black-throated tanager and a yellow-rumped tanager.

From top to bottom:

a. Back-ruffling and silent Gaping by the captive black-throated tanager in the New York Zoo.

b. and c. Head-down Postures of an adult male yellow-rumped tanager during a high intensity dispute in the wild.

they utter "Tzzheets" in series. I have seen really exaggerated Belly-fluffing only twice. In one case a wild adult male showed extreme Belly-fluffing in combination with Back-ruffling (see figure 5b) and uttered Thin Rattles after being approached by an adult female or a juvenile bird. In the other case a captive male assumed a rather low or "hunched" posture with Belly-fluffing, Crown-flattening, and slight Back-ruffling (see figure 4b), after being introduced into the cage of another pair of yellow-rumped tanagers and being



repeatedly threatened and supplanted by the male of the pair. The combination of a hunched posture with Belly-fluffing is very reminiscent of the "Fluffed Hunched Posture" of green-backed sparrows and the "fluffed postures" of many other passerines (Hinde, 1955). The latter seem to contain very strong escape components and function as appeasement. Perhaps the Belly-fluffing of yellow-rumped tanagers is also an expression of the escape tendency. (Female yellow-rumped tanagers may ruffle the feathers of the breast and belly in Bill-up Tail-up Postures in sexual situations [see page 24] but this probably is not strictly equivalent to the Belly-fluffing of males.)

Crown-flattening is less conspicuous than the feather-raising patterns and easily overlooked in the field, but it is certainly combined with a variety of other displays, including Thin Rattles, Bill-up Tail-up patterns, and "Turning-away" (see page 23), in addition to Belly-fluffing and Back-ruffling (see figures 2b, 2d, 4a, 4b, and 5a). There is no very obvious "common denominator" to all the situations in which Crown-flattening occurs. In almost all cases, however, it is shown by males in close association with (known or presumed) females at the height of the breeding season, and it can occur immediately after copulation. It may be an expression of some sexual tendency or tendencies (or a particular combination of sexual and escape tendencies).

All yellow-rumped tanagers seem to perform Tail-fanning that is very similar to the Tail-fanning of crimson-backed tanagers. Like the latter it is performed in such a very wide variety of situations that it is particularly difficult to interpret. Perhaps it is an indication of an activated escape tendency. If so it probably is performed when the escape tendency is weaker and/or in less conflict with other tendencies than when all or most Belly-fluffing is produced. It is frequently performed by individuals who are not performing any other ritualized displays (except Flicking movements) at the same time.

The patterns involving raising of the head feathers are much more conspicuous than either Crown-flattening or Tail-fanning but perhaps equally problematical.

There may be two slightly different types of Head-ruffling. In one type all the feathers of the crown are raised to a more or less extreme degree. The tips of all the crown feathers are well separated from one another. When viewed from the side the general effect is exactly the same as in the Head-ruffling of orange-rumped tanagers, illustrated by figure 4d. The top of the head appears rounded with the highest point near the center of the crown. This is usually, perhaps always,

accompanied by some raising of the feathers of the chin, throat, and cheeks. "Rounded" Head-ruffling of this type seems to be performed most frequently by birds disturbed by the presence of a potential predator. It is frequently associated with Nasal Notes and may be produced by similar motivation, i.e. when the escape tendency is stronger than the attack tendency but the latter is by no means negligible. Part of this pattern, i.e. the raising of the crown feathers, may be strictly homologous with the "Crest-raising" of green-backed sparrows and some other "emberizine" finches (see Andrew, 1961). The other type of Head-ruffling is illustrated by figure 4c. In this pattern the head does not appear to be rounded. When viewed from the side there are more or less distinct peaks at the forehead and nape as well as in the center of the crown. The feathers of the chin, throat, and cheeks also are raised, perhaps more so on the average than in the "rounded" Head-ruffling. This type of Head-ruffling may be called "angular." It occurs during many encounters between males and females but usually not in close association with successful copulations. It seems to be characteristic of situations in which both hostile and sexual tendencies are activated simultaneously and are in strong conflict with one another. It may be intermediate between "rounded" Head-ruffling and Head-fluffing.

The most typical form of Head-fluffing is illustrated by figure 3a. The feathers of the crown are raised to a very considerable extent, but their tips are not well separated from one another. When viewed from the side the head appears to be roughly square or trapezoidal, with one angle at the front of the crown and another at the back of the crown. There is no peak in the center of the crown. The cheek and throat feathers may be raised but seldom or never as much as in extreme Head-ruffling. Typical Head-fluffing usually or always accompanies Dawn Calling, especially Dawn Calling of Hoarse Flourishes or "Kioo" or "Klloo" Notes, and is rare or absent in other circumstances. A less extreme form of Head-fluffing sometimes accompanies series of "Tzzheet" Notes later in the day (see figure 3b). It seems likely that Head-fluffing is primarily or exclusively an expression of sexual motivation, but not the same sexual tendency (or combination of tendencies) as Crown-flattening. It may have been derived by exaggeration and (increased) ritualization from the more or less square but less "swollen" head-shapes frequently assumed by such species as the silver-billed tanager and the *Chlorospingus* bush-tanagers during Dawn Calling.

Yellow-rumped tanagers may have one other purely or primarily

hostile display. This was seen only during one prolonged territorial dispute between two adult males. One of the males repeatedly supplanted the other. Between supplanting attacks the aggressive male adopted a distinctive and presumably ritualized Head-down Posture. The usual form of this pattern is shown in figure 6c. The head was lowered and the neck stretched forward while the bill was pointed diagonally downward. This was accompanied by a moderate amount of Back-ruffling, with the usual drooping of the wings. The tail was lowered but apparently not fanned. The feathers of the head may have been raised, at least occasionally, but apparently never to an extreme degree. Every once in a while the tail was suddenly raised to the position shown in figure 6b, but this may have been nothing more than a balancing reaction. Both the Head-down Postures and the supplanting attacks were accompanied by many rattling patterns, usually or always Thin Rattles. This Head-down Posture is one of the more peculiar patterns of the species. It is rather different from anything observed in other species of *Ramphocelus* or other genera of supposedly closely related tanagers. It may resemble certain patterns of "emberizine" finches (Andrew, 1961), but the evidence is insufficient to determine if it is partly or wholly homologous with the latter or if it has evolved (as a social signal) independently.

The copulatory patterns and associated or related reactions of yellow-rumped tanagers were observed in only one area, near the mouth of the Rio Piedras on the Atlantic coast, in February and March of 1962. They were not studied at length simply because they were relatively rare and performed less frequently than hostile or other sexual reactions. (This seems to be characteristic of almost all the tropical members of the American "nine-primaried" songbird group).

Among the most conspicuous reactions of the species is Pouncing. It was observed five times. In each case an adult male which had been sitting on a high perch or flying high above the ground suddenly swooped down at a bird in adult female or juvenal plumage. (The males involved were different in each case. I am almost certain that all the birds that were swooped at were adult females. As far as I could tell there were no birds in the area at the time which performed typical juvenile behavior patterns.) In four out of the five cases the bird that was swooped at was flying, in an apparently unritualized manner. In the other case it was perched quietly in low scrub. In all cases the swooping male uttered rattling noises during the descent. All males uttered Thin Rattles; several uttered pure



Rattles and/or Muffled Rattles. The swoops of the males brought them very close to the females but not, I think, into actual contact. In four out of the five cases the female reacted to the swoop by flying away very rapidly. In two of these cases the male followed and a long twisting chase ensued. In the other two cases the male turned away, landed on a perch, and relaxed. After one swoop both birds landed in a tree about ten feet apart from one another. The male uttered pure Rattles and/or Thin Rattles, facing the female, while the female did silent Gaping in the direction of the male. Then the female flew away and the male did not follow. This swooping behavior of male yellow-rumped tanagers is very reminiscent of the Pouncing of male song sparrows (*Melospiza melodia*) described by Nice, 1943, but seems to be performed much less frequently. Although the accompanying Rattles indicate that some hostility is involved, the pattern may be primarily an attempt at forced copulation or rape.

Turning-away is another apparently ritualized pattern which seems to be performed only by adult males in the presence of females at the height of the breeding season. It is most common immediately after a male joins or is joined by a female. The two birds usually face one another when they first come together. But then the male may deliberately turn away and stand for at least a few seconds rigid and motionless with his tail pointing directly toward the female. In this position the male usually performs typical Back-ruffling (the ruffling may appear even before he turns) and holds his head fairly low (in any case, his head and foreparts must be more or less hidden from the female). His tail may be approximately horizontal or slightly raised. Sometimes it is fanned. Figure 2c shows a posture of this type. The male usually falls silent as soon as he turns away from the female. Only once did I hear a male utter a single note, a Hoarse Flourish, while he stood motionless.<sup>9</sup>

Two apparently successful copulations were observed. Both occurred early in the morning, approximately one half hour after dawn. The birds involved were not the same in the two performances. One performance began when the male flew into a tree where the female was already perched. He perched on a branch about ten

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<sup>9</sup> Once a male was seen to stand in a slightly more distinctive posture after Turning-away. The wings were drooped as during typical Back-ruffling, but the yellow feathers of the lower back and rump were not erected to any appreciable extent (see figure 2b). As this was the only time that a male was ever seen to perform conspicuous wing-drooping without ruffling of the yellow feathers, in any circumstance, the performance may have been nothing more than an individual aberration.



feet above her, then flew straight down on to her back. She went into a Bill-up Tail-up Posture just before he landed. Her wings were stretched out horizontally at the same time but they were not Quivered. The male began copulatory movements as soon as he landed. These seemed to be essentially identical with those of related species. The copulation itself was brief. As soon as he finished the male flew away and disappeared from view. The female remained in the Bill-up Tail-up Posture for some seconds afterwards. She also kept her wings out horizontally and performed two or three "spasmodic" bursts of very rapid Wing-quivering (definitely separated by brief periods in which the wings were held quite motionless). Then she gradually relaxed and assumed an unritualized posture. As far as I could tell both birds were absolutely silent throughout the whole performance. The other copulation began when the male flew straight on to the female's back without any preliminary perching near her. He uttered one Muffled Rattle in flight. The female went into a Bill-up Tail-up Posture as he approached. Her head and bill were pointed nearly vertically upward while her tail was raised diagonally. The feathers of her breast and belly were ruffled, but much less so than in the homologous postures of many related species. She spread her wings out horizontally but did not Quiver them. The male began copulatory movements as soon as he landed, and the copulation itself was almost as brief as the one described above. After dismounting the male perched right beside the female with his body parallel to hers and facing in the same direction. She remained in a Bill-up Tail-up Posture with her wings held out motionless. He also assumed a Bill-up Tail-up Posture (with Crown-flattening). His posture is illustrated in figure 2d. His wings were not stretched out horizontally. They were folded on his back, but one was held much higher than the other. As a result his yellow rump was revealed quite conspicuously on the side on which the wing was high. This was the side nearest the female. After a few seconds the male flew away. The female immediately came out of her Bill-up Tail-up Posture, but she kept her wings out horizontally. Then she performed three spasmodic bursts of Wing-quivering as she gradually lowered her wings (without folding them). Then she flew to another perch a few feet away. There she performed several more bursts of Wing-quivering while her wings were still drooped. Then she relaxed.

Two of the display patterns associated with copulations are of some comparative interest. The holding of the wings in an asymmetrical position after copulation may be related to the asymmetrical raising

of the wings by male crimson-backed tanagers before copulation. Wing-quivering seems to be obsolescent in yellow-rumped tanagers. It is performed less frequently than in some species of related genera. Perhaps it is on the way to complete disappearance, as it seems to have done already in crimson-backed tanagers.<sup>10</sup>

In addition to the possible cases of attempted rape described above, four reactions which may have been unsuccessful copulation attempts were observed. In all four cases an adult male flew to a presumed female uttering Thin Rattles and/or Muffled Rattles as he did so. Once the male hovered over the female's back, apparently attempting to land there. The other times the male landed beside the female. Twice the female responded by assuming a Bill-up Tail-up Posture. When this happened the male retreated at once. (Bill-up Tail-up Postures seem to be part of "soliciting" in many passerines, but they may not encourage copulatory behavior by male yellow-rumped tanagers.)

When precopulatory behavior is stopped short or cut off abruptly, without leading to actual copulation, male yellow-rumped tanagers tend to perform one or more rapid bill-wiping movements. Similar movements are performed by males of many related species in similar circumstances. This is the sort of reaction which looks, at least superficially, like "displacement."

#### DISCUSSION

Three aspects of the display repertory of yellow-rumped tanagers seem to be particularly significant:

1. The remarkable resemblance of some of the vocal patterns, especially the Rattle—Hoarse Flourish "complex," to some of the vocalizations of *Chlorospingus* species.

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<sup>10</sup> There are indications that the yellow color of the rump is essentially a non-hostile (perhaps positively sexual) sign stimulus. The contrasting black, or the combination of black with a light bill, may be a hostile sign stimulus. I have seen a wild male yellow-rumped tanager attack an adult male blue-black grassquit (*Volatinia jacarina*). Adult male blue-black grassquits have almost entirely black plumage and silvery bills. As the individual that was attacked did not seem to be doing anything to provoke hostility, it may have been attacked simply because of its appearance. If so the stimuli releasing attack may be essentially the same in both yellow-rumped tanagers and crimson-backed tanagers. If black is a hostile stimulus in both species, they differ significantly from species of certain other groups of American "nine-primaries" songbirds, e.g. honeycreepers of the tribe Dacnini. (This will be discussed in more detail in a later paper.)

The similarities are extensive and detailed enough to suggest that *Ramphocelus* and *Chlorospingus* are closely related to one another.

The two genera are kept far apart from one another in current classifications and checklists, e.g. Hellmayr, 1936; but the differences between them, e.g. in bill shape, body proportions, and the absence of bright plumage in males of *Chlorospingus*, may be nothing more than superficial adaptations to particular habitat preferences and feeding methods.

2. The large number of different types of display.

Two general features seem to be characteristic of the display behavior of many highly gregarious species of the American "nine-primaried" songbird group, and probably many other groups as well (see Moynihan, 1960 and 1963). Highly gregarious species seem to express a larger proportion of their hostility by means of display, and a smaller proportion by overt unritualized activity, than do less gregarious species. They also, in many cases, have fewer recognizably distinct types of partly or purely hostile displays or partly independent components of displays than less gregarious species. (As the great majority of displays in all species are at least partly hostile, this latter statement means, in fact, that highly gregarious species tend to have a lesser total number of types of display than less gregarious species.)

The highly gregarious yellow-rumped tanagers seem to conform to the first of these general rules but not to the second. They do express a very large proportion of their hostility by display. (It is noticeable, for instance, that they relatively seldom perform overt attack and escape movements without also performing some display, usually vocal, at the same time.) They do not, however, have a relatively small number of different types of display. They certainly have many more different types of display than such extremely gregarious species as the plain-colored tanager, *Tangara inornata* (personal observation). They even have more different types of display than the moderately gregarious and closely related crimson-backed tanagers. They seem, in fact, to have at least as many different types of display and partly independent components of displays as the very slightly gregarious green-backed sparrow (which seems to be as nearly completely nongregarious as any species of neotropical tanager or finch).<sup>11</sup>

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<sup>11</sup> The variety of different signals in the repertory of yellow-rumped tanagers is even greater than would be suggested by the number of different components alone. This is because the different components can be combined in a rather



The differences in numbers of displays between yellow-rumped tanagers and other highly gregarious tanagers may be correlated with, i.e. causally related to, differences in breeding behavior. All the other highly gregarious tanagers whose behavior has been studied in detail tend to feed and move about in groups, but they do not show the tendency to breed close together which is so conspicuous in yellow-rumped tanagers. Behavioral interactions between birds breeding in colonies or semi-colonial groups may be particularly complex (simply because the constant presence of other individuals will stimulate many incompatible tendencies, such as sex and hostility, that are stronger on the average during the breeding season than at other times of the year). A great variety of signal patterns may be necessary in order to regulate or control such complex interactions with maximum efficiency. (Another factor of slightly different order may be involved. Colonial or semi-colonial breeders such as yellow-rumped tanagers may have developed, or retained, comparatively strong aggressive tendencies in order to prevent their strong gregarious tendencies from leading to overcrowding or general promiscuity. There is evidence that a high degree of aggressiveness in itself favors the development or retention of a great variety of displays, irrespective of the social structure in which the aggressiveness is expressed. See Moynihan, 1963.)

### 3. The intergrading of the vocal patterns.

The major vocal patterns of yellow-rumped tanagers intergrade with one another more frequently and more conspicuously than the corresponding patterns of any other American "nine-primaried" songbird whose behavior has been studied. This seems to be a highly specialized character and must be adaptive. The only other groups of animals in which a similar contrast between species with intergrading vocal patterns and species with distinct, nonintergrading patterns has been recognized is the mammalian order of primates. Among primates there is evidence to suggest that the species with intergrading vocal patterns are those which are least dependent upon vocal signals *alone* for the regulation of their social behavior. Intermediate (and ambivalent) notes, produced by intergrading, have certain advantages as signals. They may convey complex messages (i.e. the precise combination of tendencies in the animal producing the notes) in very

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surprisingly large number of different ways, e.g. the combinations of one vocalization with several different types of feather-raising and of one type of feather-raising with several different types of vocalization. Different combinations of display components seem to be more common in the repertory of yellow-rumped tanagers than in those of many or most related species.



abbreviated form (i.e. coded with maximum efficiency). But they also have certain disadvantages. They may be difficult to read or decipher because of their complexity or easily confused with other (related) vocal patterns, simply because they are not always very distinctive in sound (they must resemble the other notes between which they are intermediate). These disadvantages may be avoided if the intermediate vocal patterns are usually or always accompanied by other information which will make their meaning clear. Thus among primates the species or classes of individuals that utter many intermediate or intergrading vocal patterns are diurnal and/or highly gregarious and/or tend to remain in very close contact with the other members of their own family group. Any individual of these species or classes hearing calls or notes from another individual of the same species will usually perceive visual, olfactory, or tactile signals or other stimuli from its companions and/or receive visual or olfactory clues from the physical environment at the same time. These visual, olfactory, or tactile aids should enable the receiving individual to grasp the meaning or significance of any vocal pattern, even when the latter is difficult to decipher or ambiguous in itself. (This aspect of vocalization in primates is discussed in more detail in Moynihan, 1964.) It is possible that the different types of vocal repertory in different species of tanagers are adaptive in much the same way as the corresponding types of repertory in primates. Perhaps yellow-rumped tanagers can "afford" to utter many intermediate notes simply because they are usually within sight, as well as sound, of their most important social companions, competitors, and rivals *throughout the year*. They must receive visual clues and stimuli with a larger proportion of the vocalizations to which they should respond than do individuals of other species which are more isolated during the breeding season.

#### SOME PATTERNS OF ORANGE-RUMPED TANAGERS

Two adult male orange-rumped tanagers in the New York Zoo were observed briefly during a few days of October 1958. They were labeled "*flammigerus*," and probably were hybrids between *f. flammigerus* and *f. icteronotus*. They were kept in separate aviaries. There were many other birds of different species in both aviaries, including other species of *Ramphocelus*. Both orange-rumped tanagers performed an appreciable number of displays and related or associated patterns. They became engaged in disputes with a variety of other species. They even performed a few partly sexual patterns.

One of them was particularly interested in a female silver-billed tanager, while the other seemed to have formed pair-bonds with a juvenile black-throated tanager (*R. nigrogularis*).

The orange-rumped tanagers were observed to perform Flicking movements, Gaping, Head-ruffling (see figure 4d), Back-ruffling, Belly-fluffing, and "silent song," and heard to utter Nasal Notes and Rattles. Some of these patterns, e.g. the Nasal Notes, were apparently identical with the corresponding displays of Panamanian yellow-rumped tanagers. Others differed to some (usually slight) extent. Some of the differences are listed below.

Both orange-rumped tanagers performed silent Gaping rather more frequently than the yellow-rumped tanagers kept in captivity on Barro Colorado Island. Much of this Gaping was done with the head lowered and the neck stretched forward. A Gaping bird usually faced straight toward the other bird releasing the performance. The combination of Gaping with lowering of the head and stretching of the neck may have been ritualized per se to form a "head forward threat" display like that of many other passerines (see Andrew, 1961). Once a bird in this posture looked downward. This was reminiscent of the Head-down display posture of yellow-rumped tanagers (except that the Gaping was maintained throughout).

Once a bird was seen to perform Back-ruffling that involved the black feathers of the center of the back as well as the orange feathers of the rump and lower back.

The most extreme Belly-fluffing observed is shown in figure 5c. This is considerably less extreme than the most exaggerated Belly-fluffing of yellow-rumped tanagers or crimson-backed tanagers, but it may well have been low intensity.

All the Rattles sounded like the pure Rattles of yellow-rumped tanagers.

Both orange-rumped tanagers also uttered moderately loud (but not metallic) notes that might be transcribed as "Whit" or "Tsit." They were uttered singly and in series when the birds were more or less isolated (as much as possible within the aviaries), and were not accompanied by overt indications of alarm. This would suggest that such notes are largely or completely homologous with the "Tzzheet" Notes of yellow-rumped tanagers, *not* the softer "Tsit" Notes uttered by one yellow-rumped tanager in captivity. Sometimes single moderately loud "Whit" or "Tsit" Notes were uttered immediately before and/or immediately after Rattles. Such compound calls presumably are related to the "Tzzheet"—Thin Rattle—Hoarse Flourish per-

formances of yellow-rumped tanagers. Both orange-rumped tanagers usually sat without moving while they uttered "Tsit" or "Whit" Notes, with or without Rattles.

The "silent song" patterns were performed by only one of the orange-rumped tanagers. I was told that this individual had assumed adult plumage only a few months earlier. Its "silent songs" were largely inaudible at a distance of three feet. Occasionally, one or more soft but clear "Whit" or "Tsit" notes were interjected, apparently at random, in otherwise silent "phrases."

#### SOME PATTERNS OF BLACK-THROATED TANAGERS

In addition to the single individual in the New York Zoo, a few black-throated tanagers were observed in the wild near Iquitos, Peru, in December 1958. The general social behavior of these Peruvian birds is described in Moynihan, 1962a. They were keeping together in what looked like a family group, including both adults and young, and also were associating with a family group of silver-billed tanagers. They performed a few displays, including Flicking movements of the usual *Ramphocelus* type and silent Gaping from a variety of unritualized postures. During one violent intra-specific dispute, one bird performed Gaping while its opponent kept its bill almost or completely closed, and one or both birds uttered rapid "twittering" phrases of short notes which sounded like some type of Hoarse Notes. During another intra-specific dispute, one or more birds uttered similar "twittering" series of Hoarse Notes without any sign of Gaping. Several times an adult was heard to utter series of three to eight "Whi-it" or "Wheeeet" Notes when it flew ahead of its companions. These appeared to be a type of "summons," presumably related to the Plaintive Notes of many other species, the "Tzzheet" Notes of yellow-rumped tanagers, and the "Tseeet" Notes of crimson-backed tanagers.

The individual at the New York Zoo was observed to perform similar Flicking and silent Gaping and assume "head forward threat" postures like orange-rumped tanagers. Once, when it was attacked by a barbet in the same aviary, it responded by Gaping in an upright posture and ruffling the black feathers of the upper back (see figure 6a).

All the black-throated tanagers near Iquitos uttered many loud, metallic sounding "Tsit" Notes. These were *very* similar to the "Tsit" Notes uttered by silver-billed tanagers in the same region (although perhaps slightly softer) and were uttered in similar social circum-



stances. There is some evidence that the "Tsit" Notes of these silver-billed tanagers are "Short Hostile Notes" and homologous with the Nasal Notes of crimson-backed tanagers. This may also be true of the "Tsit" Notes of Peruvian black-throated tanagers. If so, such notes are not strictly homologous with either the "Tsit" Notes of the captive yellow-rumped tanager on Barro Colorado Island or the "Tsit" Notes of the captive orange-rumped tanagers in the New York Zoo. (I might add that none of the black-throated tanagers observed near Iquitos or in the New York Zoo uttered any notes which sounded more like the Nasal Notes of other species.)

In any case it is possible that the resemblance between the "Tsit" Notes of the black-throated tanagers and silver-billed tanagers near Iquitos is an example of some kind of mimicry. This resemblance may facilitate associations between the two species, and such associations may be advantageous (to one or both species) in some circumstances. (It may be significant that the Short Hostile Notes of silver-billed tanagers in Trinidad, where black-throated tanagers are absent, are rather different in sound.) It is equally possible that the similarities between the Nasal Notes of yellow-rumped tanagers and crimson-backed tanagers facilitate associations between these two species.

The vocalizations of the captive black-throated tanager in the New York Zoo were rather puzzling. It uttered Rattles quite like those of the orange-rumped tanagers. It also uttered "Tsit" Notes, softer and less metallic than those of the Iquitos birds, by themselves alone and immediately before and/or after Rattles. These "Tsit" Notes may have been strictly homologous with those of the orange-rumped tanagers. (This particular black-throated tanager may also have been imitating, or have learned part of its repertory from, the orange-rumped tanager in the same aviary.)

#### GENERAL COMMENT

It may be useful to emphasize certain aspects of the display behavior of the genus *Ramphocelus* as a whole.

1. There is no display or combination of displays that can be considered diagnostic of the genus, i.e. that is performed by all the species of the genus and not by species of other genera.

2. All or most of the displays performed by some but not all of the species of *Ramphocelus* are also found in some species of other genera. In most cases the homologous patterns of species of other



genera are very similar to the corresponding displays of *Ramphocelus* species in form, function, and causation.

3. In view of these similarities between *Ramphocelus* species and species of other genera, it is perhaps remarkable that there are so many differences between the yellow-rumped tanager and the crimson-backed tanager. The display behavior of the yellow-rumped tanager, as a whole, seems to be as much like that of the brown-capped bush-tanager as like that of the crimson-backed tanager, while the display behavior of the crimson-backed tanager seems to be as much like that of *Tachyphonus rufus* as like that of the yellow-rumped tanager. (The behavior of *Tachyphonus* species will be discussed in a later paper.)

Comparable contrasts are found within other genera, e.g. *Saltator*, *Cyanerpes*, and *Diglossa*. It does, in fact, seem to be characteristic of many groups of American "nine-primaried" songbirds that the differences between the display repertoires of different species of the same genus are at least as great as the differences between their repertoires and those of some species of other genera.

4. The differences between the purely or predominantly sexual displays of yellow-rumped tanagers and crimson-backed tanagers are not greater than the differences between some of their other displays. Some of the patterns apparently used by males to attract mates, e.g. some Dawn Calling notes, are actually quite similar in the two species. This would suggest that much of the divergence between the display repertoires of these two sympatric species is not primarily, or not only, an adaptation to maintain reproductive isolation between them.

#### ACKNOWLEDGMENTS

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I am grateful to Mr. William G. Conway for facilitating observations of captive birds in the New York Zoo, and to Dr. Philip Humphrey and Mr. Eugene Eisenmann for checking specimens in the United States National Museum and the American Museum of Natural History.

#### SUMMARY

This is primarily a study of the behavior of yellow-rumped tanagers (*Ramphocelus flammigerus icteronotus*) observed under natural conditions in Panama.

Yellow-rumped tanagers are highly gregarious. They even associate in semicolonial groups during the breeding season.

They are highly vocal. They utter Nasal Notes, Rattles, and melodious "Kioo" or "Klloo" Notes, plus a great number of intermediate notes and calls, all or most of which intergrade with one another.

The comparatively great frequency of intermediate and intergrading vocal patterns may be a result of the extreme gregariousness of the species. Any individual hearing a call or note will usually receive visual information from its companion(s) at the same time. This will facilitate the interpretation of any vocal message, even when the latter is ambiguous or would be difficult to decipher by itself alone.

Yellow-rumped tanagers seem to have more different types of display and partly independent components of display than all or most related species. This may be correlated with their semicolonial breeding habits.

Many of the vocal patterns of yellow-rumped tanagers are very similar to patterns of brown-capped bush-tanagers (*Chlorospingus ophthalmicus*). The similarities are extensive and detailed enough to suggest that the genera *Ramphocelus* and *Chlorospingus* are closely related to one another.

There is no display or combination of displays diagnostic of the genus *Ramphocelus* as a whole. The display repertoires of some species of other genera are not more different from those of some species of *Ramphocelus* than the latter are from one another. There is some evidence that many of the differences between the repertoire of the yellow-rumped tanager and that of the sympatric crimson-backed tanager (*R. dimidiatus*) subserve other functions instead of, or in addition to, the maintenance of reproductive isolation between the two species.

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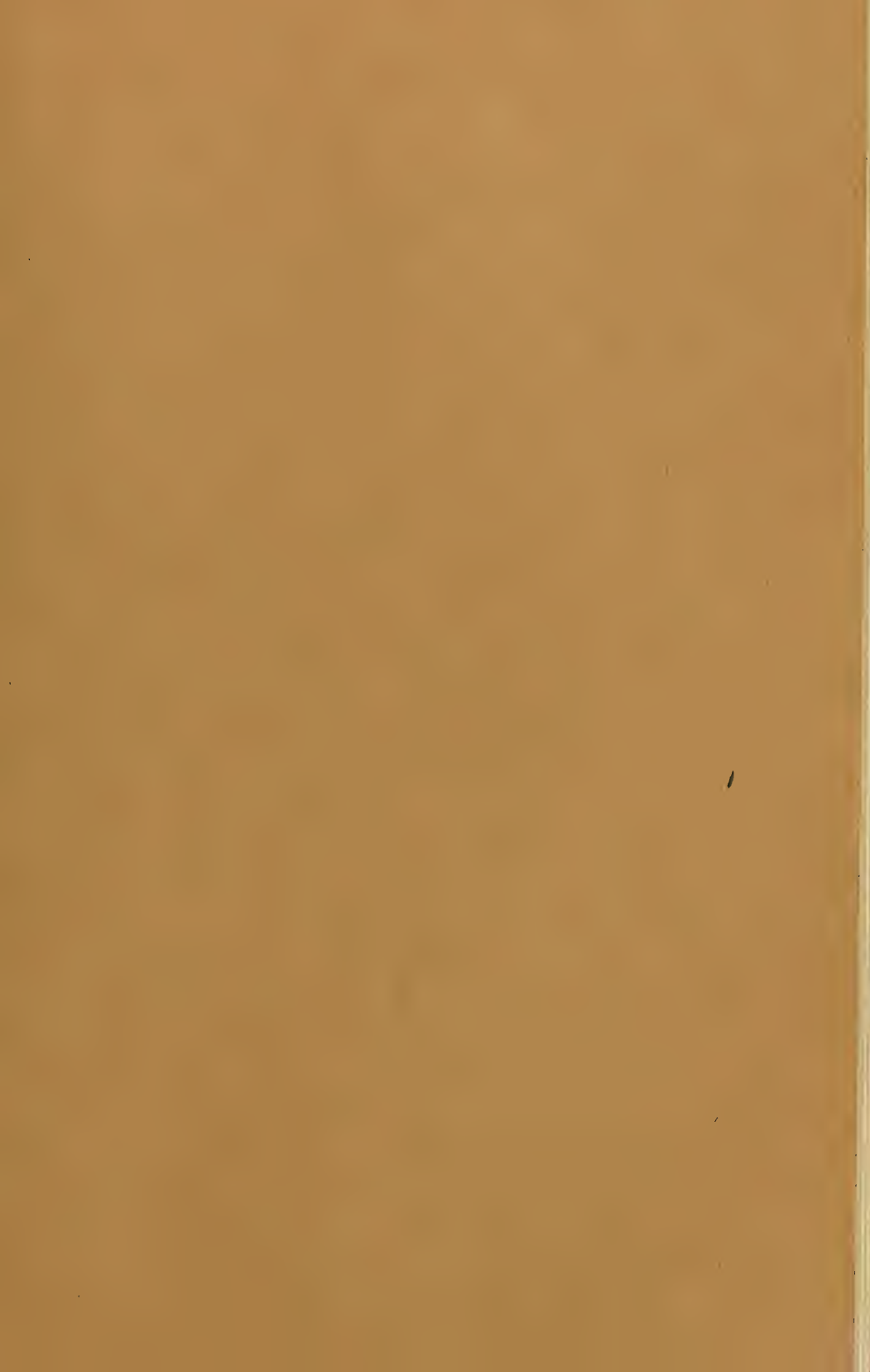
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ECHINOID DISTRIBUTION AND HABITS,  
KEY LARGO CORAL REEF  
PRESERVE, FLORIDA

(WITH 16 PLATES)

By  
PORTER M. KIER  
U. S. National Museum, Smithsonian Institution  
and  
RICHARD E. GRANT  
U. S. Geological Survey, Washington, D. C.



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CITY OF WASHINGTON  
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# CONTENTS

	PAGE
Abstract . . . . .	1
Introduction . . . . .	2
Location and methods. . . . .	2
Echinoid fauna . . . . .	5
Acknowledgments . . . . .	5
Echinoid distribution . . . . .	8
Major environments . . . . .	8
Systematic discussion of species. . . . .	12
<i>Eucidaris tribuloides</i> (Lamarck). . . . .	12
<i>Diadema antillarum</i> Philippi. . . . .	14
<i>Astropyga magnifica</i> Clark. . . . .	15
<i>Arbacia punctulata</i> (Lamarck). . . . .	17
<i>Echinometra lucunter</i> (Linnaeus). . . . .	18
<i>Echinometra viridis</i> Agassiz. . . . .	20
<i>Lytechinus variegatus</i> (Lamarck). . . . .	21
<i>Tripneustes ventricosus</i> (Lamarck). . . . .	24
<i>Echinoneus cyclostomus</i> Leske. . . . .	25
<i>Clypeaster rosaceus</i> (Linnaeus). . . . .	26
<i>Clypeaster subdepressus</i> (Gray). . . . .	28
<i>Leodia sexiesperforata</i> (Leske). . . . .	31
<i>Encope michelini</i> Agassiz. . . . .	33
<i>Plagiobrissus grandis</i> (Gmelin). . . . .	36
<i>Brissus unicolor</i> (Leske). . . . .	38
<i>Meoma ventricosa</i> (Lamarck). . . . .	38
<i>Schizaster (Paraster) floridiensis</i> Kier and Grant, new species. . . . .	50
Enemies of echinoids. . . . .	54
Relation of test shape to living habit. . . . .	55
Abnormal specimens . . . . .	56
Conclusions . . . . .	58
Literature cited . . . . .	61
Explanation of plates . . . . .	63



Charles D. and Mary Vaux Walcott Research Fund

## ECHINOID DISTRIBUTION AND HABITS, KEY LARGO CORAL REEF PRESERVE, FLORIDA

By

PORTER M. KIER, *U. S. National Museum, Smithsonian Institution*, and  
RICHARD E. GRANT, *U. S. Geological Survey, Washington, D. C.*

(WITH 16 PLATES)

### ABSTRACT

SEVENTEEN SPECIES of echinoids were found between the shore and a depth of 110 feet seaward from the living reef. All but one were encountered alive, and observed in their habitats. *Eucidaris tribuloides* (Lamarck) is solitary, widely and sparsely distributed in rocky niches and turtle grass. *Echinometra lucunter* (Linnaeus) is abundant in rock niches just below low tide, and less abundant in isolated clumps of coral and sponge on sand. *E. viridis* Agassiz is less abundant in the same habitats, and extends to greater depth on the reef. *Arbacia punctulata* (Lamarck) similarly inhabits rocky niches along the shore, and also clusters near sponges and corals elsewhere. *Diadema antillarum* Phillipi is ubiquitous, living at all observed depths in rocky niches along the shore and on the reef, in large flocks in turtle grass, but not on clean sand. *Astropyga magnifica* Clark moves in groups over open sand areas at relatively greater depth. *Lytechinus variegatus* (Lamarck) and *Tripneustes ventricosus* (Lamarck) occupy similar habitats in turtle grass, although *L. variegatus* is more abundant and its habitat includes rocky areas near shore.

The sand dollars *Leodia sexiesperforata* (Leske) and *Encope michelini* Agassiz burrow through the uppermost inch of sand, and are absent from rocky or grassy areas. Similarly, *Clypeaster subdepressus* (Gray) burrows through the upper part of the substrate, or occasionally merely covers itself with sand and shell debris and moves along the surface of the sand. The latter mode of life is normal for *Clypeaster rosaceus* (Linnaeus) which never was seen to burrow



and therefore can live in grassy areas. Less commonly it leaves the grass and moves over the surface of clean sand. *Meoma ventricosa* (Lamarck) normally burrows in areas of thick grassless sand relatively far from shore. It was observed rarely on the surface of the substrate, in grass or on clean sand, with debris held onto the test in the manner of *C. rosaceus*. *Plagiobrissus grandis* (Gmelin) burrows in clean sand, and was never observed at the surface. *Brissus unicolor* (Leske) and *Echinoneus cyclostomus* Leske live in coarse sand beneath rocks in the vicinity of the reef.

The only species not observed alive is *Schizaster (Paraster) floridiensis* n. sp., which also has been found off the coast of the island of Dominica in the southern Caribbean.

### INTRODUCTION

Echinoids are important constituents of the near-shore marine biota, contributing significantly to the food-chain and to modification of the substrate. In some areas they are among the most abundant megascopic animals. Similarly, their remains are abundant as fossils, especially in younger geologic strata, and as such they have become important indicators of the ages and environments of deposition of many Tertiary formations. These animals have been studied by zoologists and paleontologists since the beginnings of those sciences, and much has been learned about their evolution, gross areal distribution, general biology, habitat preferences, and especially their taxonomy. Nevertheless, until the invention of self-contained underwater breathing apparatus it remained virtually impossible to observe in detail the living habits and local habitat preferences of any but intertidal species. The authors are paleontologists whose prime concern is to interpret the ecology and life-habits of fossil animals, normally through recourse to the literature of biology and ecology. However, detailed data on the habits and habitats of living echinoids is scarce, therefore it was necessary to make firsthand observations.

The results of this preliminary study are presented in order to provide a broad ecological framework for further such studies in other areas, and for more detailed and comprehensive investigations of individual species.

*Location and methods.*—The Key Largo Coral Reef Preserve is an area almost completely under water which has been set aside by the governments of the United States and Florida for the preservation of a living coral reef and its surroundings (fig. 1). The administration is under the State of Florida, which has named its on-shore facilities

and the underwater portion that lies within its jurisdiction the John Pennekamp State Park. The Reef Preserve lies in the Atlantic Ocean,

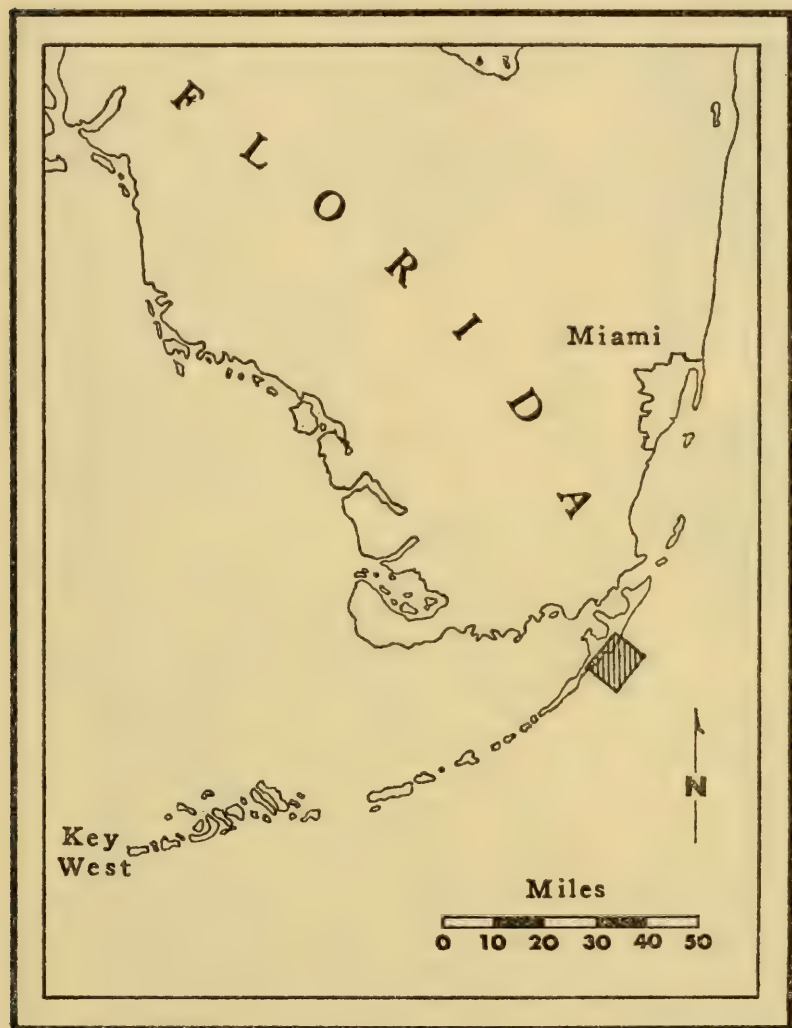


Fig. 1.—Map of southern Florida and the Keys; shaded rectangle indicates area shown on figure 2, in southern part of Key Largo Coral Reef Preserve.

southeast of the middle part of Key Largo, extending from about 1.5 miles offshore to just beyond the living coral reef about 5.5 miles offshore, for a length of about 20 miles. The area of this study ex-

tends from the shore to just beyond the outer boundary of the Reef Preserve, between the Grecian Rocks and the Molasses Reef Light, an area of about 55 square miles (fig. 2).

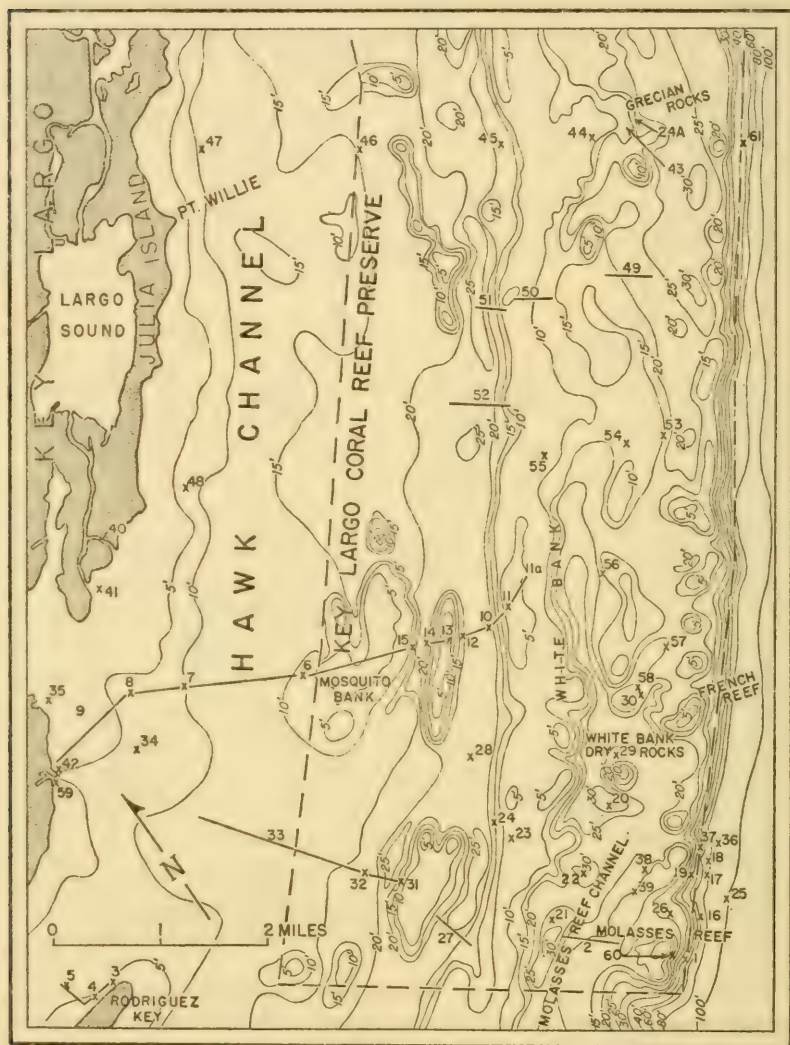


Fig. 2.—Contour map of area studied; depth contours in feet; numbers refer to stations; numbered straight lines are traverses. Map adapted from U. S. Coast and Geodetic Survey chart 1249.

Several different environments are present in this area; each that has a bearing on the distribution of the echinoids is described below

and its echinoid fauna discussed (fig. 3). Depths that were explored range from intertidal along the shore and at exposed parts of the reef, to 110 feet seaward from Molasses Reef. The investigation included the making of several traverses across the various channels, reefs, and sand flats, detailed census-taking in selected small areas, and the less detailed investigation of numerous stations in each of the various environments.

*The echinoid fauna.*—Seventeen species of echinoids were observed in the area of study. They belong to several of the major echinoid groups, and inhabit many different environments (table 1):

“Regular” echinoids

- Eucidaris tribuloides* (Lamarck)
- Diadema antillarum* Philippi
- Astropygya magnifica* Clark
- Arbacia punctulata* (Lamarck)
- Echinometra lucunter* (Linnaeus)
- Echinometra viridis* Agassiz
- Tripneustes ventricosus* (Lamarck)
- Lytechinus variegatus* (Lamarck)

“Irregular” echinoids

Holactypoida

- Echinoneus cyclostomus* Leske

Clypeasteroida

- Clypeaster rosaceus* (Linnaeus)
- Clypeaster subdepressus* (Gray)
- Leodia sexiesperforata* (Leske)
- Encope michelini* Agassiz

Spatangoida

- Plagiobrissus grandis* (Gmelin)
- Brissus unicolor* (Leske)
- Meoma ventricosa* (Lamarck)
- Schizaster (Paraster) floridiensis* new species

Living specimens of all these species were observed except *Schizaster (Paraster) floridiensis*. Although we saw only a few specimens of *Brissus unicolor* and *Echinoneus cyclostomus*, all the other species were abundantly represented by living individuals.

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TABLE 1.—Occurrence of Echinoids

Bottom type		Sand bottom	
Depth and location		Bare sand	Turtle grass
INTER-TIDAL 2-6'	NEAR SHORE		
	OFF SHORE		
NEAR SHORE 4-8'		Clypeaster rosaceus	Clypeaster rosaceus Lytechinus variegatus
INSHORE EDGE HAWK CHANNEL, RODRIQUEZ KEY 4-15'			Clypeaster rosaceus Diadema antillarum Echinometra lucunter Echinometra viridis Lytechinus variegatus
HAWK CHANNEL 10-18'			Arbacia punctulata Clypeaster rosaceus Diadema antillarum * Lytechinus variegatus
BACK REEF CHANNEL 10-20'			Arbacia punctulata Clypeaster rosaceus Diadema antillarum Eucidaris tribuloides Lytechinus variegatus Tripneustes ventricosus *
WHITE BANK 10-12'		Clypeaster rosaceus Clypeaster subdepressus Encope michelini Leodia sexiesperforata Meoma ventricosa Plagiobrissus grandis *	Clypeaster rosaceus Diadema antillarum Eucidaris tribuloides Lytechinus variegatus Tripneustes ventricosus
INTERREEF CHANNEL 15-35'		Clypeaster rosaceus Clypeaster subdepressus Encope michelini Leodia sexiesperforata Lytechinus variegatus * Meoma ventricosa Plagiobrissus grandis * Schizaster (P.) floridiensis * Tripneustes ventricosus *	Brissus unicolor * Clypeaster rosaceus Diadema antillarum Eucidaris tribuloides Lytechinus variegatus Meoma ventricosa Tripneustes ventricosus
R E E F	SHOREWARD PATCHES 5-10'		Clypeaster rosaceus
	MAIN REEF 10-35'	Clypeaster subdepressus Diadema antillarum Meoma ventricosa Schizaster (P.) floridiensis	
	SEAWARD PATCHES 110'		
SEAWARD TERRACE 80-85'		Astropyga magnifica Clypeaster subdepressus Diadema antillarum Eucidaris tribuloides Meoma ventricosa Plagiobrissus grandis * Schizaster (P.) floridiensis *	

\* Rare.

TABLE 1.—Occurrence of Echinoids

Rock bottom		
Living coral	Rock and dead coral	Broken rock
	Diadema antillarum Echinometra lucunter Lytechinus variegatus	Diadema antillarum Echinometra lucunter Lytechinus variegatus
		Diadema antillarum Echinometra lucunter Eucidaris tribuloides Tripneustes ventricosus
Arbacia punctulata Diadema antillarum Echinometra lucunter		
Diadema antillarum	Diadema antillarum Echinometra viridis	Brissus unicolor Echinoneus cyclostomus Eucidaris tribuloides
Diadema antillarum		
		Diadema antillarum

specimens. Norman F. Sohl of the U.S. Geological Survey dove with P. M. Kier on an earlier expedition to the keys during which a preliminary study of the echinoid fauna was made. Craig Pontin of the Sea Center, Key Largo, ran the boat, provided accurate determinations of location for each station, and made available his extensive and detailed knowledge of bottom conditions and depths. Herb Pontin was most kind in permitting use of his larger boat during rough weather. The State of Florida gave permission to collect specimens in John Pennekamp State Park. We thank Thomas Phelan, research assistant at the U.S. National Museum, who helped in the preparation and study of the collected specimens. The fish were identified by John E. Randall, University of Puerto Rico Institute of Marine Biology.

The manuscript was reviewed critically by Dr. J. Wyatt Durham, University of California, Dr. Peter Glynn, University of Puerto Rico Institute of Marine Biology, and Dr. Richard S. Boardman, U.S. National Museum, whom we thank for their many valuable suggestions.

#### ECHINOID DISTRIBUTION

The southern part of the Key Largo Coral Reef Preserve and its shoreward extension divide naturally into several major types of environments determined by the nature of the bottom, depth of the water, and distance from shore (table 1). These major environments form bands between and roughly parallel to the shoreline and the outer edge of the living coral reef. Hawk Channel, White Bank, and various parts of the reef have formal names (fig. 2); other areas have been given convenient field designations for purposes of this discussion (fig. 3).

#### MAJOR ENVIRONMENTS

*Intertidal (rocky shore and exposed reef).*—Rocky shore (stations 35, 42, 59, inshore end of station 9) depth (just off seawall) 2–4 feet at midtide; very steep, large rocks of dead coral, living alcyonarian and anthozoan corals, large loggerhead sponges, sparse green algae, abundant coralline algae and turtle grass extending to tidal edge. *Echinometra lucunter* is abundant at station 59, in depths as shallow as one foot at low tide; *Lytechinus variegatus* and *Diadema antillarum* also occupy the steep rock intertidal shore edge.

Exposed reef (station 38) depth 2–6 feet, high tide; gently sloping rocky bottom, rocks covered with thin algal slime. Echinoids are

*Eucidaris tribuloides* (on and under rocks), *Echinometra lucunter* (numerous in holes in rocks, and under rocks), *Diadema antillarum* (relatively small, numerous under rocks and around edges of rocks), *Tripneustes ventricosus* (one juvenile under rock). In addition, each rock that was turned over revealed several active brittle stars scurrying for cover.

*Permanently underwater, just offshore.*—(Stations 7, 8, 9, 34, 35, 48) nearly flat rock bottom covered with thin layer of calcareous sand; water depth 4-8 feet; numerous loggerhead and basket sponges, alcyonarian and large and small scleractinian corals, patches of sparse turtle grass (*Thalassia*), patches of algae. Echinoids: *Lytechinus variegatus* (in grass), *Clypeaster rosaceus* (in grass and on sand).

Rock bottom of artificial channel at station 40; depth about 6 feet, edged by mangroves, has numerous *Diadema antillarum* attaining large size, living in recesses on bottom, and on vertical rocky irregular sides, and among lower parts of mangrove roots; this is partly intertidal.

*Inshore edge of Hawk Channel.*—(Stations 33, 47) sand bottom, mostly covered with turtle grass, few bare patches; depth 10-15 feet; water typically murky; echinoids: *Lytechinus variegatus* and *Clypeaster rosaceus* abundant in grass, a few small solitary *Diadema antillarum*.

Shallows just inshore from Rodriguez Key; (stations 3, 4, 5) depth 4-10 feet; sand bottom with large areas of turtle grass (*Thalassia*), calcareous algae (*Halimeda*), merman's brush (*Pennicillus*), brown algae, widely scattered loggerhead and basket sponges, small staghorn and brain corals imbedded in sand, buried clams (*Arca*), holothurians, brittle stars, and echinoids: *Diadema antillarum* (solitary and in groups of up to 50), *Lytechinus variegatus* (in grass), *Echinometra lucunter* and *E. viridis* (under clumps of sponge, coral, and shells), *Clypeaster rosaceus* (in grass and on bare sand). Detailed survey of 100 square feet in sparse turtle grass at station 3 (depth 4 feet) produced the following echinoids:

*Lytechinus variegatus*—7 alive

*Echinometra lucunter* and *E. viridis*—5 alive, under clumps

*Clypeaster rosaceus*—4 alive, 2 dead

*L. variegatus* and *C. rosaceus* live on the sand bottom, individuals about 1.5-2 feet apart but without apparent segregation as to species. About 20 feet from this surveyed area, in an area 15×5 feet, at the same depth (4 feet) were 90 small and medium size *D. antillarum*, in one group of 50, one of 20, and two groups of about 10 each, living on the sand bottom in short, sparse turtle grass (pl. 2, fig. 4).



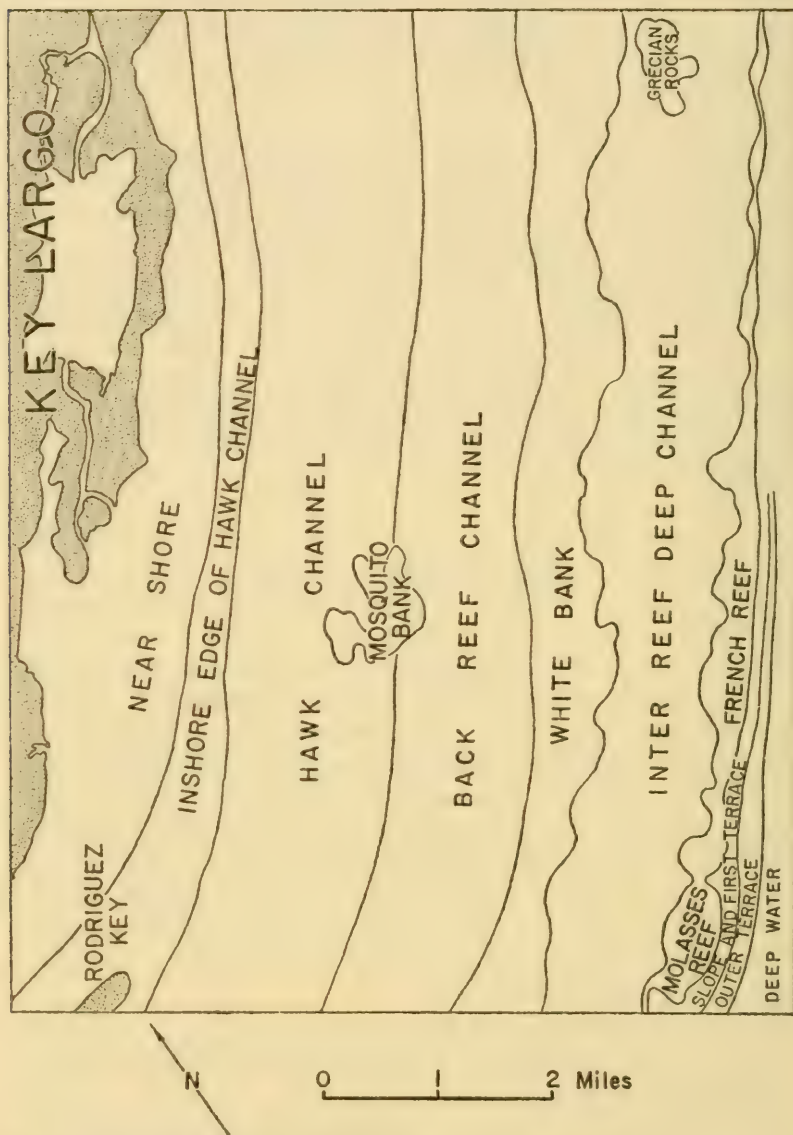


Fig. 3.—Locations of major environments mentioned in text.

*Hawk Channel and its offshore edge.*—(Stations 6, 32, 33, 46) cloudy water, fine sand and silt bottom with dense turtle grass; depth 10-18 feet; numerous worm burrows and mounds, small free-living scleractinian corals, crabs, starfish (*Linckia*); echinoids: *Lytechinus variegatus* (very abundant, about 1.5-2 feet apart, small), *Arbacia punctulata*, *Diadema antillarum* (rare), *Clypeaster rosaceus* (less abundant than *L. variegatus*).

*Back reef channel.*—(Stations 10, 12, 14, 15, 24, 27, 28, 31, 51, 52) sand and silt bottom, grassless patches and patches of turtle grass (small reef patches discussed separately); depth 10-26 feet (shoaling to reef patches); water normally cloudy, turtle grass covered with "dust"; small sponges and scleractinian corals, numerous holothurians, worm burrows; echinoids: *Eucidaris tribuloides* (few), *Lytechinus variegatus* (abundant), *Tripneustes ventricosus* (few), *Arbacia punctulata* (few), *Diadema antillarum* (many, in groups of 3-5), *Clypeaster rosaceus*. Station 14 is clean sand with no echinoids.

*Reef patches in back reef channel.*—(Stations 13, 15, 27) hard rock bottom with patches of thin sand; depth 5-10 feet; many corals and sponges, fish; echinoids: *Echinometra lucunter* (on coral), *Arbacia punctulata* (under edge of sponge), *Diadema antillarum*, *Clypeaster rosaceus* (on sand patches).

*White Bank.*—(Stations 11, 11a, 23, 24, 45, 50 and offshore ends of stations 27, 51, 52) depth 10-12 feet, 3-6 feet over shoals; broad areas of white, rippled sand, patches of sparse turtle grass; echinoids: *Eucidaris tribuloides* (few), *Lytechinus variegatus* (abundant, in grass), *Tripneustes ventricosus* (few in grass), *Diadema antillarum* (few, in grass and on rock at station 50), *Leodia sexiesperforata* (in sand), *Encope michelini* (in sand), *Clypeaster subdepressus* (in sand), *C. rosaceus* (in grass and on sand), *Plagiobrissus grandis* (in sand), *Meoma ventricosa* (in sand).

*Interreef channel.*—(Stations 2, 20, 21, 22, 29, 30, 39, 44, 49, 53, 54, 56, 57, 58) depth 15-35 feet; broad areas of clean, white, rippled sand, with large irregular, slightly elevated patches of turtle grass; echinoids in sand areas: *Encope michelini*, *Leodia sexiesperforata*, *Clypeaster subdepressus*, *C. rosaceus* (near edges), *Meoma ventricosa* (large), *Plagiobrissus grandis*, *Schizaster* (*Paraster*) *floridiensis* (dead), tiny *Lytechinus variegatus* and *Tripneustes ventricosus* in clumps. Echinoids in turtle grass: *Eucidaris tribuloides*, *Lytechinus variegatus*, *Tripneustes ventricosus*, *Diadema antillarum*, *Clypeaster rosaceus*, *Brissus unicolor* (dead), *Meoma ventricosa* (small).

*Living coral reef.*—(Stations 1, 26, 43, 60) depth 10-25 feet, high relief; abundant niches in both living and dead parts of reef, in-

habited by large individuals of *Diadema antillarum*. Sandy patches in large depressions and grooves contain few *Clypeaster subdepressus*. *Echinoneus cyclostomus* and *Brissus unicolor* live under slabs of reef debris in and near the reef.

*Outer edge of reef, and sandy terrace*.—(Stations 16, 18, 19, 37, 61) depth 25-50 feet; tongues of sand extending from sandy terrace up through steep-sided grooves in lower edge of reef; sand fairly clean, with rocky patches, burrows by burrowing fish, some algae, broad ripples. Echinoids in sand: *Clypeaster subdepressus* (buried deeply), *Meoma ventricosa*, *Schizaster* (*Paraster*) *floridiensis*, *Brissus unicolor*, *Echinoneus cyclostomus*. Echinoids in holes in rock: *Diadema antillarum* (abundant), *Echinometra viridis* (one specimen).

*Level sand flats beyond reef*.—(Stations 17, 17a, 36) depth 80-85 feet; bare sand with thin cover of algae in patches, rocky holes of burrowing fish, small piles of rock supporting sponges and small corals; echinoids: *Eucidaris tribuloides*, *Diadema antillarum* (small, among rock and sponges), *Astropyga magnifica* (in groups, on sand), *Clypeaster subdepressus* (small, many dead, few alive), *Meoma ventricosa*, *Plagiobrissus grandis* (dead), *Brissus unicolor*, *Schizaster* (*Paraster*) *floridiensis* (dead).

*Deep water beyond 85-foot terrace*.—(Station 25) depth 105-110 feet; large mounds of living coral, with sponges, fish, crinoids, basket stars, mounds about 50 feet long, 12 feet high, surrounded by coarse sand of shell and calcareous algal debris. Very large *Diadema antillarum* in niches in coral mounds; no echinoids observed in sand.

#### SYSTEMATIC DISCUSSION OF SPECIES

Descriptions, synonymys, and illustrations of the species discussed below can be found in Mortensen (1928-1951).

##### Order CIDAROIDA Claus

##### Family CIDARIDAE Gray

##### Genus EUCIDARIS Pomel

##### EUCIDARIS TRIBULOIDES (Lamarck)

Plate 2, figures 1-3; text figure 7

This large brown urchin is easily recognized by its long thick spines arranged in 10 vertical series. It has a globular shape and is locally known as the mine or satellite urchin. An adult is approximately 100 mm. in horizontal diameter with its spines, 50 mm. without. The naked test is characterized by straight, narrow poriferous zones with only two vertical rows of pore-pairs in each ambulacrum, and broad interambulacral areas with 10 vertical series of large tubercles.



*Occurrence.*—*Eucidaris tribuloides* was found only seaward from the "back-reef channel," although it was found much nearer shore farther south off Molasses Key. It is widespread but not abundant in the Coral Reef Preserve, occurring in depths from intertidal to at least 85 feet. It lives on sandy or rocky bottoms (pl. 2, figs. 1-3) but was not found on clean sand where grass or algae were absent. This species lives in the same kind of environment as *Lytechinus variegatus*, *Tripneustes ventricosus*, and *Arbacia punctulata*, but its distribution seems to be most nearly coincident with that of *T. ventricosus* in this area; it is not as widespread as *L. variegatus* (fig. 7). Normally it is solitary and well camouflaged, so in light of observed occurrences elsewhere in the Keys, we believe that an intensive search for this species would extend its range in the Coral Reef Preserve to the region nearer shore.

This species was found at stations 1, 2, 10, 11, 12, 22, 24, 30, 36, 38, 51, 52, and 53.

*Behavior.*—*Eucidaris tribuloides* lives unburied, on rocky (pl. 2, fig. 1) or sandy bottoms (pl. 2, figs. 2, 3) but not in areas of clean, grass-free sand. Specimens were found in dense and sparse turtle grass, normally with their upper and lateral primary spines covered by sheaths of living algae which render the animal nearly invisible (pl. 2, figs. 2, 3). Individuals living in grass normally were solitary, whereas those living on rock, under the overhang of a sponge or coral were more typically clustered in favorable niches. Some lived under slabs of rock in shallow water, and in deeper water where slabs had fallen into deep "grooves" between spurs of the reef.

Mortensen (1928, p. 404) reports that this species feeds on algae and Bryozoa. Its abundant presence in areas of turtle grass leads us to suspect that it also eats grass, although no direct observations of its feeding habits were made. This species is relatively immobile during the day; its nocturnal behavior is unknown. We observed no trails, and did not see undisturbed specimens in motion.

## Order DIADEMATOIDA Duncan

### Family DIADEMATIDAE Peters

#### Genus DIADEMA Gray

#### DIADEMA ANTILLARUM Philippi

#### Plate 2, figures 4-7

This black urchin has extremely long, slender hollow spines the tips of which are mildly venomous. The urchin is very large, many adults



being more than 200 mm. in horizontal diameter with spines, 100 mm. without. The bare test is flattened and the apical system and medial areas of the interambulacra are depressed. The ambulacra are narrow, inflated with the pore-pairs in two fairly straight series in each area. Spines of mature specimens are black, but those of juveniles are annularly banded black and white. Kristensen (1964, p. 15) reports that adults with gray or banded (or white) spines occur in areas of low light intensity, either deep or turbid water.

*Occurrence.*—*Diadema antillarum* is the most ubiquitous echinoid in the area of the Coral Reef Preserve. It occurs in the entire depth range studied, and extends from intertidal slopes of South Sound Creek leading from Largo Sound, to a depth of 110 feet on the seaward side of the main reef, and undoubtedly much deeper. Mortensen (1940, p. 274) reports it from depths as great as 1,200 feet. It was found among mangrove roots in South Sound Creek (station 40) and in irregularities in the limestone bottom of that creek, in sparse grass on open sand in large flocks near Rodriguez Key, in denser grass in Hawk Channel where the water is cloudy with suspended silt, in isolated reef patches within the sandy areas, in clear water at all depths on the main part of the reef, on sand terraces beyond the reef, and on discontinuous reef mounds in deep water beyond the reef. The only environment from which *D. antillarum* was absent is open grassless sand, the areas primarily inhabited by sand dollars and *Meoma ventricosa*.

This species was found at stations 1, 3, 4, 10, 11, 11a, 12, 13, 15, 16, 17, 17a, 18, 22, 25, 26, 27, 28, 31, 32, 36, 38, 40, 43, 50, 52, and 59.

*Behavior.*—*Diadema antillarum* remains relatively immobile during the day. It occupies niches and recesses in the reef or other rock, rests among mangrove roots (even on nearly vertical sides of creeks), hides under rock slabs in shallow water where dead reef is broken by wave action, or in deeper water between reef masses, or it gathers into clusters and spends the day on the sand among sparse turtle grass and other vegetation. Specimens were found around the bases of isolated sponges or corals, and even living inside the cups of larger basket sponges.

Individuals remain in their niches, gently waving their long spines (or having them waved by the surge of water), with small white mysid shrimps swimming among the spines. Upon approach of

danger, presumably sensed by motion or the shadow cast by the potentially dangerous object, *D. antillarum* begins to wave its spines rather rapidly. When the potential danger is a diver, they seem to point many of the spines at him; presumably this is their reaction to other dangers as well. Specimens that are in the open on grassy sand group their upper spines into five cone-shaped bundles and point them at the intruder, after the fashion observed in *Astropyga magnifica* (pl. 1).

Shroeder and Stark (1964) report that *D. antillarum* becomes much more active at night, leaving its niches and wandering about on the reef. Presumably the groups that rest on the grassy sand during the day also become active and more mobile during the night. Other similarities in habit suggest that perhaps the groups remain intact as they move, as do clusters of *A. magnifica* during the day.

A few individuals were seen living singly on grassy sand, away from reef mounds or other places with available niches. Many of these isolated specimens (pl. 2, fig. 5) were small, with the black and white banded spines characteristic of juveniles. A few adults also were seen alone on sand, but this mode of life seemed to be more typical of the juveniles.

#### Genus *ASTROPYGA* Gray

#### *ASTROPYGA MAGNIFICA* Clark

Plate 1, figures 1-5

This echinoid is striking in appearance with its large test (205 mm. in horizontal diameter including spines) and its radiating color pattern. Under water the interambulacra are yellow, the ambulacra brown with brilliant iridescent blue spots bordering the ambulacra. At the surface in natural light unfiltered by the water, the specimens have purplish red (mallow) ambulacra and yellow-white interambulacra. The spines are banded with the same colors. A large anal tube was present on all the living specimens. In shape and size of its test, length and thickness of its spines, this species strongly resembles *Diadema antillarum*, but is easily distinguished by its color.

*Occurrence.*—*Astropyga magnifica* was found only on the sand terrace on the seaward side of the reef, at a depth of 80-85 feet. Mortensen (1940, p. 207) reports it from a depth of 88 meters off Dry Tortugas, Fla. We observed it on nearly flat grassless sand which

was bound in places by patches of algae. The vegetation was sparse, and the topography unbroken except by small sponges and corals, and by the burrows of fish which piled pebbles, shells, and echinoid tests around the entrances of their burrows.

Too few samples were obtained to establish the range of this species in this area, but extensive searches at depths near 65 feet, and briefer searching at 110 feet revealed no specimens. After the first specimen, a juvenile, was found on the 85-foot terrace, a return to that depth produced a good collection, so we infer that the species at least does not live in shallower depths; Mortensen's report indicates that it does inhabit deeper waters.

This species was found at stations 17a and 36.

*Behavior.*—Mortensen (1940, p. 207) emphasized the extreme rarity of *Astropyga magnifica* in collections made by dredge hauls, and correctly deduced that its distribution was spotty because individuals grouped together and traveled over the surface of the sand in small groups. He was precisely correct. This species is highly mobile; it was observed moving across the sand flats single-file in groups of two to five, at a speed of approximately 3 feet per minute. Only one isolated individual was found, a juvenile at station 17a; all others were in groups.

This species moves about on its relatively short ventral spines, with all other spines radiating rather uniformly, although waving slightly with motion of the animal. Small fish, identified by J. E. Randall as a species of the cardinal fish *Apogon*, swim among the spines, keeping up with the echinoids as they move along (pl. 1, fig. 4). The anal sac is fully inflated (pl. 1, figs. 1-5), and the iridescent blue spots along the edges of the ambulacra reflect enough light to appear to glow (pl. 1, figs. 2, 3, 5). Upon the approach of danger, presumably sensed by changes in light intensity, the spines group together into five cone-shaped bundles, thus producing a strong and formidable defense (pl. 1, figs. 1-3, 5).

The gregarious habits, acute sensitivity to changes in light, waving and then bundling of spines, are modes of behavior that recall *Diadema antillarum*. That species is much less mobile during the day, normally remaining in groups on the open sea bottom or hidden in niches in coral, sponge, or rock. *D. antillarum* is active at night, however, and then its behavior is yet more strikingly similar to that of *A. magnifica* (Schroeder and Stark, 1964, p. 133).



## Order ARBACIOIDA Gregory

## Family ARBACIIDAE Gray

## Genus ARBACIA Gray

**ARBACIA PUNCTULATA (Lamarck)**

Plate 2, figures 8-9; plate 10, figure 5; text figure 4

This dark brown urchin is characterized by its long slender spines and circular ambital outline. An adult is approximately 90 mm. in horizontal diameter with spines, 45 mm. without. The area around the apical system is naked and there are usually four large periproctal plates. The dead test is reddish brown, with narrow ambulacra, and pore-pairs arranged in simple vertical series. The tubercles on the interambulacra are of the same size and are arranged in oblique series slanted up to the middle of each area. This species can be confused with *Echinometra lucunter* from which it is distinguished by its longer slenderer spines and round test, and with *Diadema antillarum* from which it differs in having thicker solid spines, and a smaller, higher test with a larger peristome.

*Occurrence.*—*Arbacia punctulata* was found primarily in areas of turtle grass, commonly associated with *Lytechinus variegatus* and *Tripneustes ventricosus*. During the day it stays in the shadow of an overhanging sponge or clump of coral (pl. 2, figs. 8, 9) although rarely it was merely in grass like the above two species. The species also occurred rarely on sandy areas with little or no turtle grass, although there it stays near corals or sponges.

This species was rare in the area of study. Its range apparently coincides rather closely with that of *Tripneustes ventricosus*, but more observations would be necessary in order to establish its limits precisely (fig. 4). It was found in the "back-reef channel" and in Hawk Channel, in depths ranging from 10 to 20 feet.

Sharp and Gray (1962, p. 309) report *A. punctulata* living on rocky bottom in about 12 to 20 feet of water off the coast of North Carolina. We encountered large numbers along the rocky shore of Molasses Key, a few miles south of the Coral Reef Preserve. Similarly, Kier has found it on the rocky coast of Dominica in the Lesser Antilles. Only one specimen was found in a rocky habitat in the Key Largo Coral Reef Preserve, exposed and uncovered on bare rock within a large grassy area at station 51. The species obviously inhabits a variety of environments, but seems to have a clear preference for



niches that offer some protection, either from predators or from sunlight (Sharp and Gray, 1962).

This species was found at stations 24, 27, 46, and 51.

*Behavior.*—*Arbacia punctulata* was not observed to cover itself with objects from the substrate. Sharp and Gray (1962) studied its reaction to various kinds of light, including sunlight, and concluded that it tends to negative phototaxis, although much less strongly than *Lytechinus variegatus*. They report also that *A. punctulata* is highly variable in its response to light, with some specimens remaining at water level during low tide, in the full light of the sun. This variability would account for our finding the species clustering under overhanging edges of coral or sponge, and also finding rare individuals on bare rock or uncovered in sparse grass.

### Order ECHINOIDA Claus

#### Family ECHINOMETRIDAE Gray

##### Genus ECHINOMETRA Gray

##### ECHINOMETRA LUCUNTER (Linnaeus)

Plate 16, figures 1-4

The living test is reddish to dark brown, usually slightly oblong, with adults from 80 to 100 mm. long although a few specimens are considerably larger. The spines are long and slender, but moderately thick near their bases. The bare test has large tubercles, two rows of which are larger in each interambulacrum and ambulacrum. The pore-pairs are arranged in arcs, and the peristome is large. This species can be confused with *Echinometra viridis* Agassiz (distinguished below) and with *Arbacia punctulata* (Lamarck). It differs from *A. punctulata* in having thicker spines, usually an oblong test, fewer large tubercles, and many periproctal plates.

*Occurrence.*—*Echinometra lucunter* was found in shallow water (2-8 feet), both near shore and on shoals far from shore. Normally it was on hard bottom, either among slabs of dead reef limestone or on small patch reefs in sandy areas. Some were found in sand away from hard substrate, but these were near sponges or small corals, or under clumps of shells, coral, and sponge. The species ranges from the shoreline to exposed parts of the reef. It was found among the rocks along the shore at station 60, and was present in sand in shallow water near Rodriguez Key. In addition, many specimens were found on rock in the shoreline intertidal zone farther south at Molasses Key, where it was found to a depth of 10 feet.

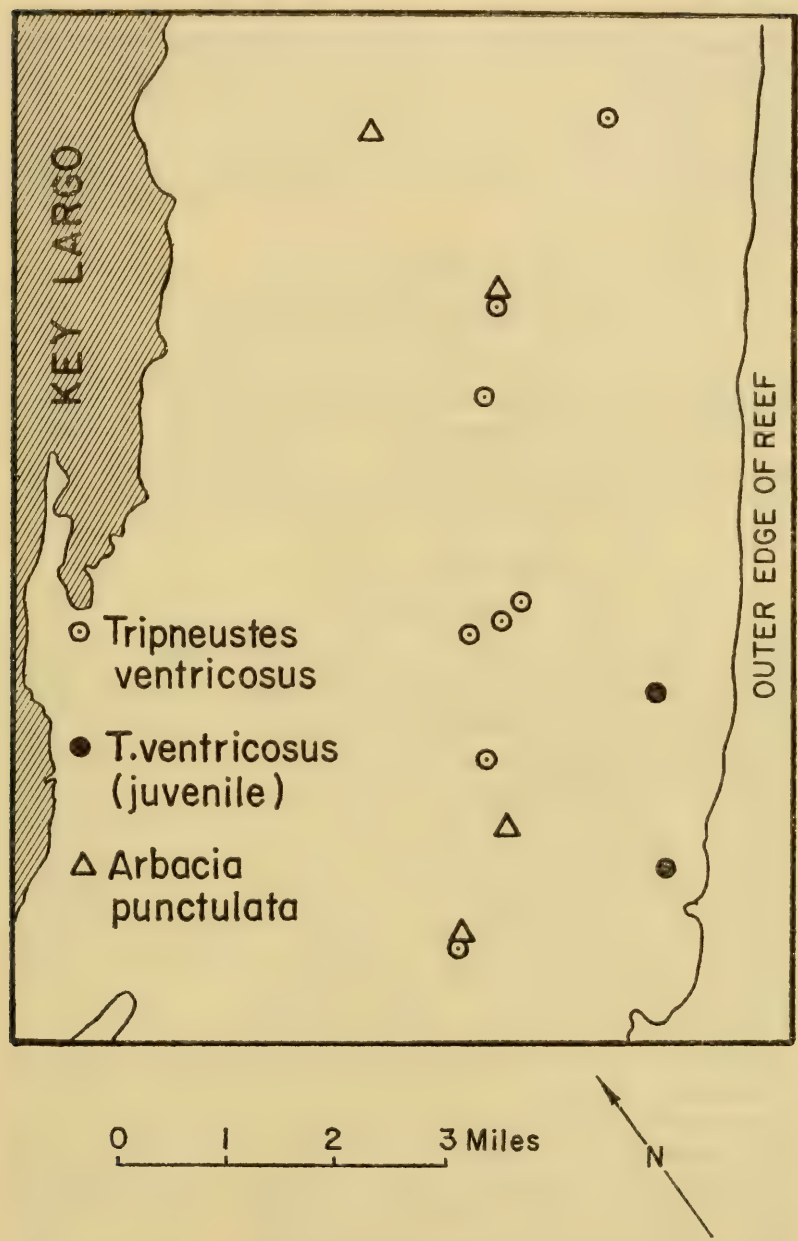


Fig. 4.—Sketch map of area studied, showing distribution of *Tripneustes ventricosus* and *Arbacia punctulata*.

This species occurs at stations 3, 13, 15, 38, and 59.

*Behavior*.—This species lives in protected niches. It inhabits holes or shallow recesses in rock, clings to the bases of sponges or coral heads, works its way under detached slabs of rock, or gets under clumps of shell and broken coral that are bound together by growths of algae and sponge. It has been found in the same environments, living closely associated with *E. viridis*, although the depth range of that species is greater.

The species was seen in great numbers living in holes in rock at station 60 and along the shore of Molasses Key, but did not appear to be trapped in the holes. Some regular echinoids are reported to enter small holes in rock as juveniles, and to enlarge the holes as they grow, finally becoming too large to pass through the entrance. *E. lucunter* inhabited holes and niches with openings large enough to permit exit; possibly they leave their protected habitats at night, and travel over the substrate as does *Diadema antillarum*.

#### ECHINOMETRA VIRIDIS Agassiz

##### Plate 10, figure 6

This species is very similar to *E. lucunter* but differs in having a smaller test, purple, gray, or blue tips on its spines, and fewer spines in the apical system. Both species occur together at some localities.

*Occurrence*.—*Echinometra viridis* was found in shallow water associated with *E. lucunter*, and also as deep as 40 feet on the main reef. In the shallow areas it was on rock or in sandy areas in clumps of shell and coral debris held together by growth of algae and sponge. One specimen was found in deeper water on rock at the edge of the reef. Its range extends from the shoreline (observed at Molasses Key, not in the area of this study) to the outer edge of the main reef; from intertidal to 40 feet and possibly deeper.

This species was found at stations 3 and 37.

*Behavior*.—Specimens living in the shoreline intertidal zone on Molasses Key were in holes in the rock. These holes appeared to be large enough to permit the urchin to enter and leave. Specimens living on sandy bottom in the area of study, just off Rodriguez Key, clustered together with individuals of *E. lucunter* among clumps of coral and shell debris bound together by living sponge. In these two shallow water habitats the two species of *Echinometra* lived together, with no apparent differences in habitat or behavior. Further research into this matter is intended, to examine the basis upon which they

are classed as separate species. For purposes of this paper they are considered separate, following Mortensen (1943, p. 365).

The one specimen that was found at the depth of 40 feet was in an elongate hole in the edge of a spur on the offshore side of the main reef (station 37). Although the specimen was difficult to remove from its niche, the aperture of the hole appeared to be sufficiently large to allow the animal to enter and leave freely.

Genus *LYTECHINUS* Agassiz

*LYTECHINUS VARIEGATUS* (Lamarck)

Plate 3, figure 1; text figure 5

The color of the test and spines of this species ranges from green, to red, purple, or white. An adult is approximately 90 mm. in horizontal diameter with spines. The bare test is high domed with smoothly curving sides, and a relatively small peristome. The ambulacra are moderately wide with the pore-pairs arranged in two series in each ambulacrum; each series with the pore-pairs in units of three. The pedicellariae are very conspicuous on a living specimen. The tubercles in the interambulacra are small and arranged in horizontal rows with approximately four in each half-interambulacrum. This species is distinguished from *Tripneustes ventricosus*, a species associated with it and somewhat similar in appearance, by its generally smaller test, variable color, more conspicuous pedicellariae, more numerous and shorter spines, and more compactly arranged pore-pairs in each poriferous zone.

*Occurrence.*—*Lytechinus variegatus* was abundant in areas of turtle grass, rare on bare sand near turtle grass and on alga encrusted rock along the shoreline, and absent from broad expanses of clean, grassless sand. It occurred in water ranging in depth from about 4 to 35 feet (fig. 5). Sharp and Gray (1962, p. 309) report its presence on shelly sand bottom off the coast of North Carolina, and its absence from grassy areas. Our findings are more similar to those of Clark (1933) who found this species in grass off Puerto Rico, and Moore, et al. (1963) who also found it in grass and absent from clean sand or gravel off Key Largo. Clark (1933) found juveniles living under and among rocks outside of grassy areas. We found them living similarly, along with juveniles of *Tripneustes ventricosus*, in sandy areas near grass patches, clustered together in aggregates of shells, algae, and especially small sponges. Extensive search of the adjacent grassy areas revealed only one juvenile *L. variegatus*.



Moore et al. (1963, p. 24) state that *L. variegatus* is intolerant of suspended silt in the water. However, we found the species to be abundant in the Hawk Channel where the water is continuously cloudy with suspended silt, at least during the summer (C. Pontin, personal communication).

The pattern of distribution of *L. variegatus* is remarkably similar to that of *Clypeaster rosaceus*, another grass-dwelling species (figs. 5, 6). On the other hand, it shows little overlap with the distribution of *C. subdepressus* or *Meoma ventricosa*, two species that prefer the clean sand habitat, and apparently prefer to live somewhat farther off shore.

According to Moore, et al. (1963) the minimum depth range of this species may be determined by two factors. One is that specimens exposed at low tide are seized by gulls which carry them to a height and drop them to crack them and expose their edible insides. The other is that the species is remarkably sensitive to short ultraviolet rays, which are filtered out by a few inches of water, as shown by Sharp and Gray (1962). Therefore, the net effect is to keep the population of *L. variegatus* confined to depths greater than those exposed at low spring tides.

The maximum depth at which this species lives probably is determined by the depth range of turtle grass (*Thalassia*), which is about 35 feet (Moore, et al., 1963). We found the species only in waters shallower than that depth, and essentially inshore from the "interreef deep channel."

This species was found at stations 2, 3, 4, 6, 7, 8, 9, 10, 11, 22, 24, 27, 28, 29, 30, 31, 33, 35, 46, 48, 51, 52 and 59.

*Behavior.*—*Lytechinus variegatus* lives above the surface of the sand, moving over the sand and the turtle grass, and climbing up among the blades of grass. Dissections of several specimens, and observation of activities of others, confirm that this species feeds mainly on turtle grass (Moore, et al., 1963).

This species, like some other nonburrowers, covers its test with objects from the bottom, holding them by its tube feet (pl. 3, fig. 1). Broad objects that cover much surface seem to be preferred. Individuals that live near shore nearly uniformly hold one or more mangrove leaves onto the test, and farther from shore where mangrove leaves are scarce, some individuals managed to find one. Others use complete clam valves, or other large fragments of shell, and many use the blades of turtle grass for cover. Experiments by Sharp and Gray (1962) suggest that this species covers itself to avoid sunlight, al-

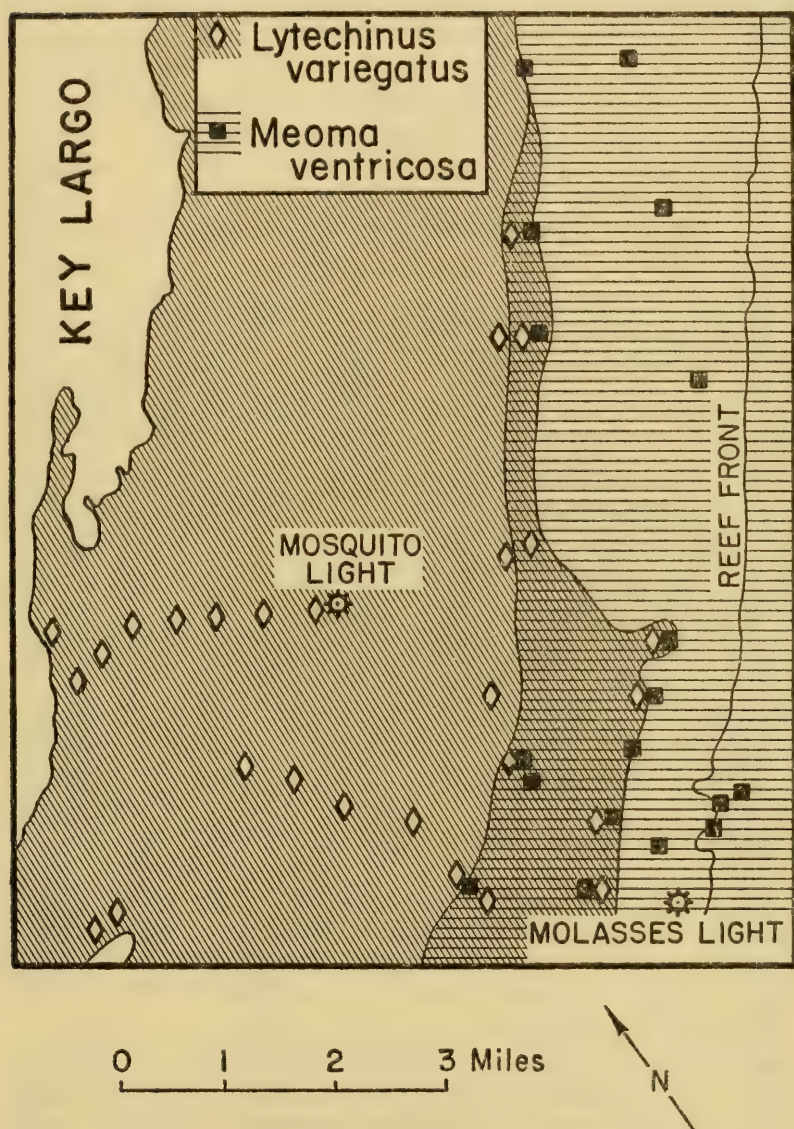


Fig. 5.—Map of area studied, showing only slightly overlapping ranges of grass and rock dwelling *L. variegatus* and sand dwelling *M. ventricosa*.

though the practice also produces a camouflage that appears to be effective and probably necessary during the daylight hours (for further discussion, see *Clypeaster rosaceus*).

## Order TEMNOPLEUROIDA Mortensen

### Family TOXOPNEUSTIDAE Troschel

#### Genus *Tripneustes* Agassiz

#### **TRIPNEUSTES VENTRICOSUS (Lamarck)**

Plate 3, figure 2; text figure 4

The test of this urchin is large—an adult approximately 110 mm. in horizontal diameter. It is brown and has numerous short, white spines. The bottom of the test is relatively flat, the top domed with smoothly curving sides. The bare test is characterized by broad ambulacra with six vertical rows of pore-pairs in each area. The interambulacra are slightly wider than the ambulacra and have many small tubercles arranged in horizontal rows. This species resembles *Lytechinus variegatus* with which it is associated and often confused, but differs in its generally larger test, persistent brown color in living specimens, less conspicuous pedicellariae, and more numerous and shorter spines. Its bare test is distinguished by its white color, and its more widely separated pore-pairs in each poriferous zone.

*Occurrence.*—*Tripneustes ventricosus* was found in grassy areas on sand bottoms. Its habitat is similar to that of *Lytechinus variegatus*, but seems to be more restricted in this area. Where the two species occur together, *T. ventricosus* is much less abundant. *L. variegatus* occurred at nearly all stations where turtle grass was abundant, but *T. ventricosus* was found only in the offshore grassy areas, on the White Bank, in the "back-reef channel" and in the "interreef deep channel" (figs. 3, 4). Depth does not appear to be the controlling factor, because the species was found in waters from 5 to 35 feet deep, a range very similar to that of *L. variegatus*.

Immature individuals about an inch in diameter were found on open sand near an extensive patch of grass at station 30, clustered together with immature *L. variegatus* in clumps of algae, broken shells, and small sponges and sponge fragments. Similar juveniles were found under rocks in only 5 feet of water at station 38, in absence of *L. variegatus*. Lewis (1958, p. 607) found mature specimens as well as immature ones on rocky bottoms off the coast of Barbados, B.W.I. *Lytechinus variegatus* was absent from this habitat in the study area and has not been reported with certainty from Barbados.



Lewis (1958) mentions the similarity in occurrence and habitat of these two species, but apparently some rather important differences in requirements also exist.

This species was found at stations 10, 11, 12, 27, 28, 29, 30 (juveniles), 38 (juveniles), 44, 51, and 52.

*Behavior.*—*Tripneustes ventricosus* lives on the sandy bottom among the turtle grass, and also climbs up the grass blades for a short distance above the bottom. According to Lewis (1958) it feeds almost exclusively on algae that grows on and among the rocks near shore. We made no systematic observations on the feeding habits of this species, but its association with *L. variegatus* in turtle grass, and its habit of climbing in the grass, indicate that it may eat turtle grass as well as algae. However, blades of *Thalassia* are frequently coated with a thin floral slime and it may be that *T. ventricosus* climbs on the grass in order to feed on the slime. Lewis reports that it rejects calcareous algae such as *Halimeda*. Kier has observed the same species living on rock near the shore of the island of Dominica, in an environment similar to that described by Lewis off Barbados. There likewise the available food was algae growing upon rock.

The habit of covering the test with shells, leaves, or other objects is much less strongly developed in this species than in *L. variegatus* (pl. 3, fig. 2). Individuals of the two species living within a foot or two of one another exhibited greatly differing amounts of cover, with *T. ventricosus* normally nearly uncovered, and *L. variegatus* ranging from sparsely covered to almost entirely concealed. Small individuals on the other hand, seemed to seek protected places under rocks, or in clumps with other small specimens (of this species and *L. variegatus*) with elaborate coverings of shells, sponges, and other objects in an intricate tangle. It would be interesting to discover whether they can drop or abandon this cover at night, and regain or reconstruct it each day, as reported for normal size *L. variegatus* by Sharp and Gray (1962).

## Order HOLECTYPOIDA Duncan

### Family ECHINONEIDAE Wright

#### Genus ECHINONEUS Leske

#### ECHINONEUS CYCLOSTOMUS Leske

#### Plate 15, figure 1

The only holectypoid found, this species is easily identified because of its large oblique peristome, with the large periproct situated just



posterior to it. A live specimen is white with very short spines and red tube-feet. Most of the specimens are small, around 30 mm. long, elongate, with narrow, simple poriferous zones, and small, equal-size tubercles. The species occurs with *Brissus unicolor*, from which it is easily distinguished by lack of petals, lower test, shorter spines, oblique peristome, and position of periproct near the peristome.

*Occurrence.*—Dead tests of *Echinoneus cyclostomus* were found on the sand below Molasses Reef and Grecian Rocks, among debris eroded from the reefs. These occurrences are well offshore, in depths from 20 to 40 feet. Mortensen (1948, p. 78) reports that this species lives among slabs of rock, normally clinging to undersurfaces, and eats organic material adhering to rather coarse grains of sand and shell fragments. It has been found in waters as deep as 350 feet.

We found few living specimens of this species; these did not seem to be clinging to the undersurfaces of rocks, but appeared to be living in coarse sand beneath the rocks. Unfortunately, the surge of waves removed the specimens from their habitats as soon as the rocks were overturned, so it was not possible to observe the echinoid in place.

Dead tests were found at stations 19 and 43, living specimens at station 60.

## Order CLYPEASTEROIDA Agassiz

### Family CLYPEASTERIDAE Agassiz

#### Genus CLYPEASTER Lamarck

#### CLYPEASTER ROSACEUS (Linnaeus)

Plate 4, figures 1-7; plate 6, figure 7; text figure 6

The test of a living specimen is dark brown, elongate, with inflated petals of equal length. An adult is approximately 130 mm. long, and is deeply invaginated around the mouth. Locally, this species is called a sea biscuit. It is a distinctive species and is easily distinguished from *Clypeaster subdepressus*, a species often occurring near it, by its much higher test, impressed mouth, and darker color.

*Occurrence.*—*Clypeaster rosaceus* lives in areas of thick sand, either in grassy areas or on relatively grassless patches within grassy areas. It is most characteristically associated with *Lytechinus variegatus* and *Tripneustes ventricosus* in the turtle grass, but also was found commonly with *Clypeaster subdepressus* and *Meoma ventricosa* in the cleaner sand areas near grassy patches. Its range extends from near shore to just inshore from the main body of the reef, and some speci-

mens were found in sandy patches that supported a growth of grass within the reef. The species was found in depths ranging from 4 to 40 feet, and its abundance did not seem to be directly affected by depth of water, but rather by the presence of turtle grass.

The distribution of this species (fig. 6) slightly overlaps with that of *C. subdepressus*. The two species occur together in the southern part of the area investigated, where irregular patches of grass and grassless sand are interspersed.

This species was found at stations 2, 3, 4, 6, 7, 8, 9, 10, 11, 11a, 12, 13, 15, 19 (dead), 20, 21, 22, 23, 24, 26, 27, 29, 30, 33, 34, 44 (dead), 45, 47, 48, 50, 51, 52, and 53.

*Behavior*—*Clypeaster rosaceus* does not burrow in the sand, but travels on its surface. Normally it lives in fairly dense turtle grass, where the tangled root systems just below the surface of the sand prevent effective burrowing (pl. 3, fig. 3). Where individuals of this species wander away from grass onto clean sand, they remain on the surface and do not burrow.

This species normally covers the upper surface of the test with locally available coarse objects (pl. 4, figs. 1-7). The grassy habitat provides a ready supply of blades of turtle grass, and the majority of individuals used them for cover (pl. 4, figs. 1, 3, 6, 7). Most also attached a few shells or shell fragments to themselves (pl. 4, figs. 3, 7) along with the grass or mangrove leaves and a little sand. Those that were found away from the grass on sandy patches used shells, shell fragments, sponges, and sand grains (pl. 4, figs. 2, 4, 5), but some that were in relatively clean sand immediately adjacent to grassy patches used a combination of grass and shell debris (pl. 4, figs. 1, 2, 4, 7). *C. rosaceus* is rare on sand that is completely free of grass, but when a specimen wanders far from its normal habitat it does cover itself with sand exclusively, although it sorts it and uses the coarsest grains (pl. 4, fig. 5).

The purpose of the habit of holding grass, shells, or other objects to the test has been a subject for controversy. Sharp and Gray (1962) conducted a series of experiments on *Lytechinus variegatus* and *Arbacia punctulata* to determine whether the habit of heaping shells onto the test was related to sensitivity to light. They conclude that *L. variegatus* is negatively phototactic, and that the habit of heaping shells and other objects onto the test in the daylight is definitely related to that character. They cite Boone (1928) to the contrary, who contended that the purpose of the covering habit was to effect camouflage. More studies such as that by Sharp and Gray, on more different kinds

of echinoids, are necessary before it can be concluded that the habit of covering is for one purpose only, or that it is for the same purpose in all species. The cover of debris employed by *C. rosaceus* is elaborate compared to that of *L. variegatus* (pl. 3, fig. 1), and no matter what the triggering mechanism may be (e.g. sunlight) the debris serves as a remarkably effective camouflage, at least to the human eye. Species in which the covering habit has been studied drop the shells and grass each night, and pick up a new supply each day shortly after sunrise (summary in Nichols, 1964, p. 406). If *C. rosaceus* also does this, it would greatly enhance the effectiveness as camouflage, as local objects would be picked up each day. As mentioned above, individuals observed in grass used grass for cover, those on shelly sand used shells; all seemed to employ sand grains to a minor extent.

#### CLYPEASTER SUBDEPRESSUS (Gray)

Plate 5, figures 1-6, 8; plate 6, figures 1-10; plate 15, figure 8; text figure 6

This echinoid has a large, low test with only slightly inflated petals, a flat lower surface, and is yellow brown to tan in color when alive. It has no perforations (lunules) or indentations at its margin, which immediately distinguishes it from the sand dollars with which it is often associated. It differs from *Clypeaster rosaceus* of this genus which is often found nearby, in its flattened test with less inflated petals, flat lower surface, and lighter color.

*Occurrence.*—*Clypeaster subdepressus* was found in sandy areas with little or no grass or filamentous algae, normally where the sand was deep. Isolated specimens were encountered in small sandy basins within reefy areas where only 6 to 8 inches of sand overlay hard substrate. Apparently it prefers depths somewhat greater than those normally inhabited by the sand dollars, *Leodia sexiesperforata* and *Encope michelini*, because it is not consistently present on the broad sandy expanses in shallow water on the White Bank. Instead it is most frequent in the large sandy areas of the "interreef deep channel" in depths between 15 and 35 feet (fig. 6). Relatively small dead tests were abundant around the nests of burrowing fish, offshore from the reef at depths as great as 85 feet; living specimens were rare and small at that depth. The limits of depths at which live or dead specimens of this species were encountered are 12 and 85 feet, although the greatest abundance of living specimens occurred between 15 and 35 feet.



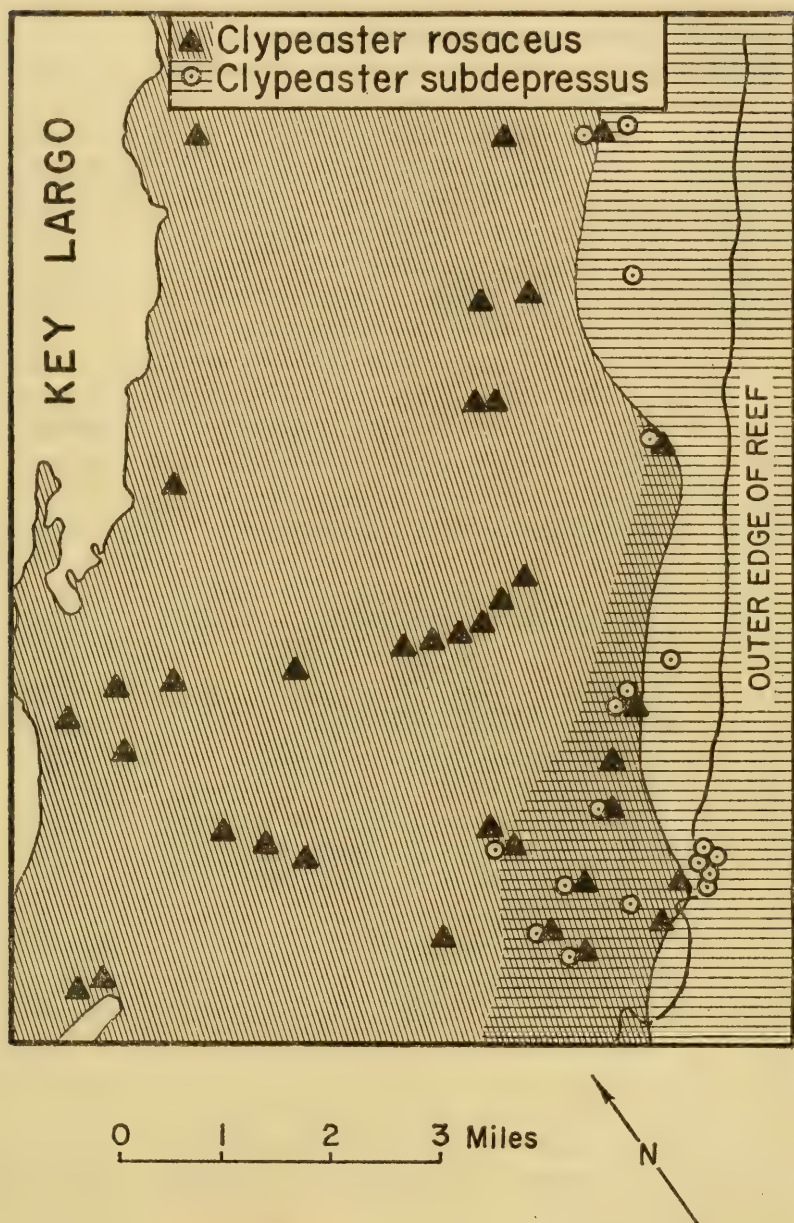


Fig. 6.—Map of area studied, showing distribution of *Clypeaster rosaceus* and *C. subdepressus*. Their ranges overlap in offshore areas where patches of grass and clean sand are intermixed.



This species was found at stations 17, 17a, 18, 19, 20, 21, 22, 23, 30, 36, 37, 39, 43, 44 (dead), 49, 53, 57, 58, and 61.

*Behavior.*—*Clypeaster subdepressus* burrows through grassless sand with its dorsal surface buried as deeply as 1 inch below the surface, or it moves along the top of the sand in areas where various algae tend to bind the sand, or where much of the sand is composed of coarse shell fragments. When it remains unburied, moving upon the surface of the sand, it covers itself with a layer of sand, shell fragments and other debris which it carries along as it moves (pl. 6, fig. 8). Normally shell fragments, leaves, or other coarse material are carried over the apical area, and finer sand over the remainder of the test.

When excavated from the sand, this species can re-bury or re-cover itself in about 6 to 12 minutes. The speed of burial, and of righting when overturned, seems to be related to size, with the smaller specimens accomplishing these activities somewhat faster than the larger ones. The manner of re-burial is illustrated on plate 5, figures 1-6, 8. The animal begins to move forward slowly, at the same time bringing sand up over the anterior and anterolateral parts of the test by means of the numerous locomotor spines that are abundant around the periphery, and the podia that are concentrated in the ambulacral areas of the dorsal surface, distal to the tips of the petals. The major portion of the sand on the test is brought up along these anterior areas, but at the same time the podia in the areas behind the two posterior petals also bring up sand grains in thin layers. The main two sheets of sand move back, coalescing with one another along the midline of the test, while two smaller, thinner sheets of sand move anteriorly from the posterolateral corners. Thus the test is effectively buried when all the sand sheets meet, which is accomplished before the animal has moved forward its own length.

This species can right itself after being overturned, although it does this in a different direction and at a slower rate than either *Leodia sexiesperforata* or *Encope michelini*. Small specimens manage to right themselves significantly faster than large ones. In one experiment where three specimens were placed near one another on their dorsal surfaces, a small one turned itself over and was buried before two larger ones raised themselves to 45 degrees (pl. 6, figs. 1-6). Sand is brought up onto the oral surface of an overturned specimen by the locomotor spines at the periphery, and the podia in the ambulacral areas. The sand comes up along one side, or one anterolateral area, thus this side is dug down into the sand. As it digs, increasing numbers of locomotor spines and podia on the oral surface are

brought into contact with the sand, and as that side digs in, the other is raised. It takes 45 minutes to an hour to achieve a vertical position, but once that is achieved, the remainder of the turnover, and complete burial are accomplished in an additional 5 to 15 minutes.

This sidewise method of overturning contrasts to that of *Leodia sexiesperforata* and *Encope michelini* which right themselves by turning on their anterior edges. Reasons for the differences probably are in the shapes of the tests, and the patterns of concentrations of spines. *L. sexiesperforata* and *E. michelini* are essentially circular, or at least their anterior portions are evenly arcuate. *C. subdepressus* is elongate, narrowest at the anterior, and has long, relatively straight sides with numerous locomotor spines along the edges, and in two interambulacral concentrations that radiate to the sides. The petal area of *C. subdepressus* projects high above the major portion of the test, and an overturned specimen that rests on this high convex hump tends to lean to one side. If all spines move, those in contact with the sand will begin to dig in, and they are the spines along the down side of the tilted test.

## Family MELLITIDAE Stefanini

### Genus LEODIA Gray

#### LEODIA SEXIESPERFORATA (Leske)

Plate 7, figures 6-8; text figure 7

This sand dollar is characterized by its very low test with thin margins, six slotlike lunules, and short petals of equal length. An adult is approximately 80 mm. in horizontal diameter and is yellow to light brown when alive, white when dead and denuded of spines. It differs from the other sand dollar associated with it, *Encope michelini*, in having a smaller thinner test, lighter color, shorter petals, and six perforations, rather than the five indentations and one perforation of *E. michelini*.

*Occurrence.*—*Leodia sexiesperforata* was found in areas of open sand where grass and filamentous algae were scarce or absent. The sand normally was rather deep (at least 1 foot) and at most localities its surface was strongly rippled, although on calm days the ripples were rapidly destroyed by burrowing of this and other species of echinoids. The species was most abundant on the broad calcareous sand expanses of the White Bank, nowhere as abundant as the other discoid species, *Encope michelini* and *Clypeaster subdepressus*

(fig. 7). The observed range extends from the shoreward edge of the White Bank to the sand patches just shoreward of the main reef (the area termed the interreef deep channel). Depths at which living specimens were found range from 10-25 feet, although dead tests were found on banks as shallow as 3 feet, and in the sand offshore from the reef at station 17a at 85 feet.

This species was found at stations 11a (dead), 17a (dead), (20) (dead), 23, 30, 39 (dead), 44, 45, 49, 55, 56, and 57.

*Behavior.*—*Leodia sexiesperforata* moves anteriorly through the sand at a depth of about 1 inch below the surface, just slightly deeper than the observed depth of burrowing of *Encope michelini*. Goodbody (1960, p. 80) observed the species near Jamaica at times burrowing so shallowly that its outline was discernible from above, and at other times burrowing somewhat deeper. The individual moves forward by means of locomotor spines which occur around the periphery of the test and in concentrations in the interambulacral areas of the ventral surface. The dorsal surface is covered with numerous short, club-shaped spines, and slightly shorter mucus-secreting spines (Goodbody, 1960, p. 83). These are used to pass sand grains up onto the dorsal surface. When a specimen is excavated from the sand it reburies itself in 5 to 7 minutes, normally accomplishing complete burial before having moved anteriorly more than one-half its own length. Burial is achieved partly by pushing forward into the sand, but mostly by passing sand grains onto the dorsal surface by the two kinds of spines. The grains are moved up along the anterior and the anterolateral edges, and passed backward over the test in two sheets which coalesce over the middle of the test (pl. 7, figs. 6-8). A few grains appear to be passed upward through the lunules, but these do not seem to play a large part in covering the test with sand.

*Leodia sexiesperforata* rights itself after being overturned by moving anteriorly or slightly anterolaterally into the sand. Locomotor spines are most densely concentrated along the anterior peripheral edge and in the two anterolateral interambulacral areas of the ventral surface (Goodbody, 1960, fig. 1). Action of these spines tends to move the oral surface into the sand at an increasingly steep angle until the test is vertical. Then the animal continues its forward motion and, by the aid of gravity, it is rapidly righted from the vertical position, and buried almost concurrently.

Goodbody (1960) described the mechanism by which food particles are moved toward the mouth of this species. Cilia at the bases of the club-shaped and the mucus-secreting spines on the dorsal surface set



up centrifugal currents that move the particles to the periphery and to the lunules. Cilia at the bases of spines on the ventral surface set up centripetal currents that are especially strong in the radial food tracts, moving the food particles medially toward the mouth. Thus the animal collects any food particles contained in any of the sand through which it passes, regardless of whether that sand passes over its ventral or oral surface.

Genus ENCOPE Agassiz

ENCOPE MICHELINI Agassiz

Plate 5, figure 7; plate 7, figures 1-8; plate 15, figure 7; text figure 7

When alive this sand dollar has a dark brown to reddish brown test covered with very short, dense spines. The test is flat, with one large slotlike lunule between the posterior petals, and usually five indentations in the ambulacra at the margin. An adult is approximately 100 mm. long. It is distinguished from the other sand dollar associated with it, *Leodia sexiesperforata*, by its larger, thicker test, longer petals, darker color, and presence of ambulacal indentations at the margin rather than perforations. It is similar to *E. emarginata* (Leske), with which it has been confused, but differs in having its adapical surface elevated posterior to the apical system whereas, in *E. emarginata* the test is flattened adapically. Furthermore, the indentations of *E. emarginata* are usually closed whereas those of *E. michelini* are open, where present. All the specimens we collected off the Keys had indentations, but they are absent on many of the specimens from the Gulf of Mexico. Thomas F. Phelan, research assistant at the U.S. National Museum, is currently making a study of the variation in these characters in the Carribbean and Gulf *Encope*.

*Occurrence.*—*Encope michelini* was found only in areas of deep sand with little or no turtle grass or filamentous algae. The surface of the sand normally is marked by large ripples up to 4 inches high and 12-16 inches between crests, although these are a function of wave oscillation and are rapidly destroyed by the echinoids on calm days. The species normally burrows through the upper surface of the sand, rarely covering its upper surface to a depth of more than one-quarter inch. Normally *E. michelini* is associated with *Leodia sexiesperforata* on the broad sandy reaches of the White Bank (fig. 7). Although it is much more abundant than *L. sexiesperforata*



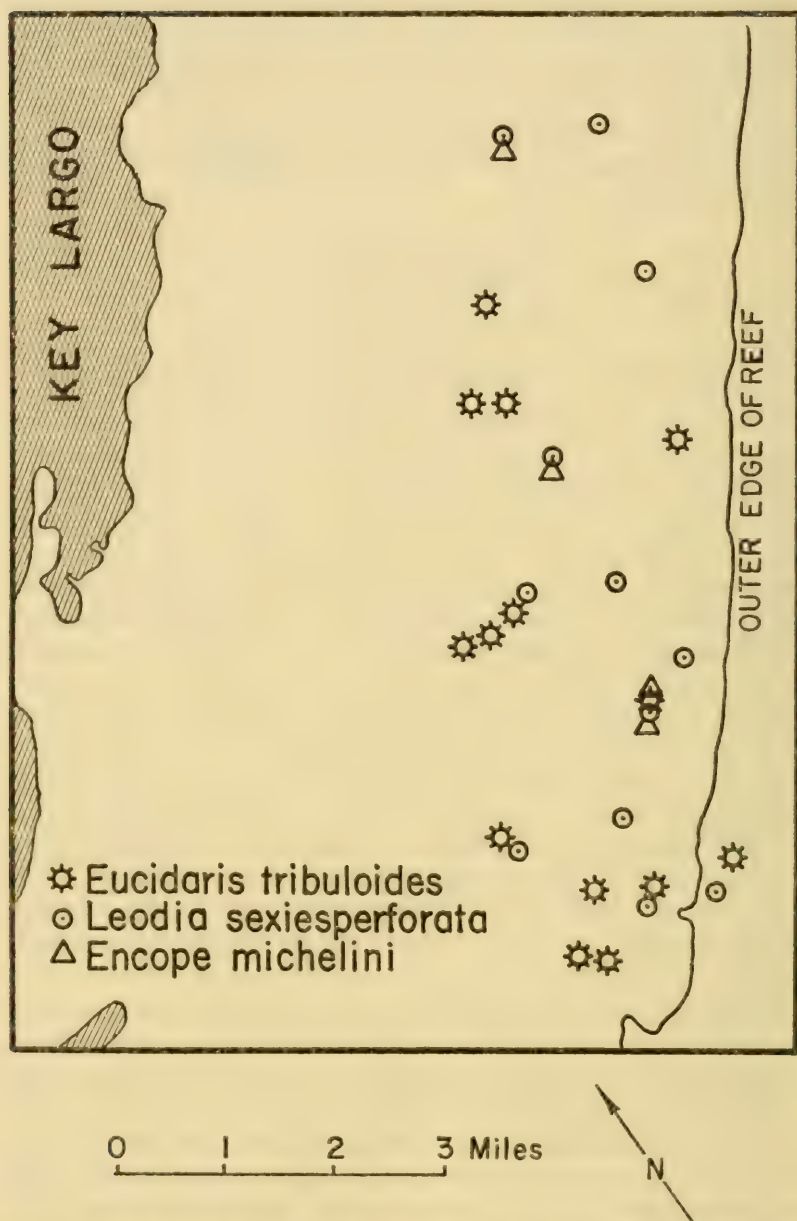


Fig. 7.—Map of area studied, showing distribution of *Eucidaris tribuloides*, *Leodia sexiesperforata*, and *Encope michelini*.

wherever it occurs, it was found only at a few localities. The range of depth of *E. michelini* in this area is between 10 and 20 feet.

This species was found at stations 23, 30, 45, 55, and 58.

*Behavior.*—*Encope michelini* is the most active of the clypeasteroids in this area. When actively burrowing it moves anteriorly through the upper surface of the sand at the rate slightly less than an inch per minute, a speed about twice that of *Leodia sexiesperforata*. It buries itself in about four minutes which is about half the time required by *L. sexiesperforata* and about a fourth of the time required by *Clypeaster subdepressus*. The outlines of most specimens are plainly visible as they move through the sand, and the trails that they leave have two low parallel lateral ridges produced by the posterolateral notches, and occasionally a median one produced by the posterior lunule (pl. 5, fig. 7).

The distribution of spines in this species is similar to that described for *L. sexiesperforata* by Goodbody (1960). The dorsal surface has only club-shaped and miliary spines; all ambulatory spines are around the periphery of the test and in radiating concentrations in the inter-ambulacral areas of the oral surface, and one transverse concentration just posterior to the posterior lunule. Therefore, the manner of burial and of turning over is similar in the two species. *E. michelini* buries itself by passing sand grains onto the dorsal surface in two coalescing sheets from the anterior and the anterolateral edges. These grains are moved progressively toward the posterior end by nonambulatory spines, and the test is effectively covered by sand before it has moved anteriorly more than three-fourths of its own length (pl. 7, figs. 6-8). Similarly, when this species is turned onto its dorsal surface, it rights itself by the same activity of ambulatory spines that normally produces forward motion. Inasmuch as these spines are concentrated on the periphery and on the oral surface of the test, the result is to bury the anterior portion of the test progressively deeper, pulling the test into an increasingly upright position (pl. 7, figs. 1-5) until it turns over. Then as it continues this motion of spines, gravity brings an increasing number of the ambulatory spines into contact with the sand, and the animal moves anteriorly through the sand into the normal position.

Feeding habits of this species were not observed, but the distribution of spines, podia, lunules (and notches), and food tracts is so similar to that of *Leodia sexiesperforata* that it undoubtedly feeds in the same manner.

## Order SPATANGOIDA Claus

## Family BRISSIDAE Gray

## Genus PLAGIOBRISSUS Pomel

## PLAGIOBRISSUS GRANDIS (Gmelin)

Plate 8, figures 1-6; plate 15, figures 2, 3

This species is characterized by its large low test, often more than 200 mm. long, tan color, and extremely long spines which curve back over the upper surface. The bare test is distinguished by the large tubercles on the upper surface, the four slightly depressed curving petals of unequal length (anterior shorter) the narrow plastron, and the thinness of the plates of the test. It differs from the other large spatangoid, *Meoma ventricosa*, with which it is often associated, by its lower, lighter test, long spines and large tubercles on the upper surface, lighter color, and narrower plastron.

*Juvenile morphology.*—A denuded specimen only 35 mm. long (pl. 15, fig. 2) was collected at locality 30. This specimen differs from an adult in many of the same ways that young *Meoma ventricosa* (described below) differs as a juvenile. It is relatively higher and less angular than the adult, its petals are less depressed, and the periproct is not visible adorally. The posterior petals are much shorter proportionately, extending only half the distance from the apical system to the margin. This contrasts to the proportionately long petals in adults which extend more than two-thirds that distance. The anterior petals are more divergent, and all petals are relatively wider and straighter in the young specimen. The peristome is larger relative to the size of the test, and the labrum less strongly developed. Unfortunately, no spines are preserved on this small specimen, so it is impossible to determine the relative change in their length with growth of the test. Genital pores are present in this small specimen, suggesting that *P. grandis* reaches sexual maturity at a smaller size than *M. ventricosa*.

*Occurrence.*—*Plagiobrissus grandis* is found in sandy areas where grass and algae are sparse or absent, associated with other sand dwellers such as *Meoma ventricosa*, *Clypeaster subdepressus*, *Encope michelini* and *Leodia sexiesperforata*. Specimens of this species are relatively rare (or at least, infrequently found) so their habitat could not be determined accurately; they seemed to be most common at the edges of the grassless areas,

The species was found only well offshore, from the White Bank

outward to the sandy terraces beyond the main reef. It occurred in depths from 12 to 85 feet, although only dead tests were found at the greater depths. It was present only in relatively deep sand, not in the shallow basins of sand between reef spurs, or patches within reef masses.

This species was found at stations 17 (dead), 17a (dead), 20 (dead), 23, and 30.

*Behavior.*—*Plagiobrissus grandis* burrows through the sand, buried just beneath the surface or as deeply as 2 inches. The long spines on its dorsal surface lie back as the animal burrows anteriorly, but stand straighter with the tips reaching the surface of the sand when forward motion ceases. The trail left by this species is less conspicuous than that of *Meoma ventricosa*, because it burrows deeper than that species. However, weak trails were visible, although normally mistaken for less fresh trails of *M. ventricosa*. Living specimens were discovered by digging at the ends of these trails, normally with the expectation of finding *M. ventricosa*.

When excavated, *P. grandis* moved rapidly over the surface of the sand with a zig-zag or "fishtailing" motion, at a speed of about 1 foot in 3 seconds. After moving about 3 feet away from an antagonist, or to a patch of sand suitable for burrowing, it begins to bury itself in a manner similar to that of *M. ventricosa*, only much more rapidly. It moves sand away from its ventral surface (pl. 8, figs. 1-3) and up along its sides into two crescentic mounds. When its dorsal surface is lowered nearly to the surface of the sand, it brings sand up onto that surface (pl. 8, figs. 4, 5), thus becoming effectively covered before the two lateral crescents of sand actually coalesce over the test. It takes only about 3 minutes to bury to a depth of about half the thickness of the test, and another 5 minutes to descend nearly to the level of the surface of the sand. Complete burial can be accomplished in 10 minutes or slightly more or less, depending upon the individual. The animal does not attempt to move forward until burial is complete or nearly so.

*Predation.*—Moore (1956) reports that *P. grandis* is frequently preyed upon by species of the helmet conch, *Cassis*. Many of the dead tests in our collection show the small circular hole that is the mark of predation by a gastropod. Dead tests and living specimens were most abundant at station 30, and there two specimens of *Cassis* were observed, a large one about 12 inches long, and a smaller one 4 inches long that was buried with its dorsal surface about 4 inches below the surface of the sand. These associations led us to suspect that *Cassis*



probably preyed upon *P. grandis* by burrowing, a surmise supported by Moore's extensive observations on this activity.

Genus **BRISSUS** Gray

**BRISSUS UNICOLOR** (Leske)

Plate 15; figures 4, 5

This small spatangoid, usually around 50 mm. long, has an elongated test inflated posteriorly, a blunt anterior margin, and a rather pointed posterior margin. The living test is white to light tan, has short spines, and very obvious black pedicellariae. Only four petals are present, the anterior pair are short and diverge 180 degrees. This species differs from the only other small spatangoid found with it, *Schizaster* (*Paraster*) *floridiensis*, by its more elongate test, shorter spines, longer posterior and shorter anterior petals, and less depressed anterior ambulacrum.

*Occurrence*.—This relatively rare species was found living under rock slabs in and near the reef. Dead tests were found in sandy areas near the reef, except for one found near an almost completely disintegrated shipwreck supporting an incipient growth of coral, sponge, and algae that probably was the ecological equivalent of a small reef patch. Living specimens on the reef occurred in about 15 feet of water, but dead tests were encountered in depths from 18-80 feet.

Mortensen (1951, p. 512) suggested that the species lives buried, which accounts for its apparent rarity. We found it living under rocks, but could not determine confidently whether it was clinging to the undersurfaces of the rocks, or was in the sand beneath them. The ease with which they drifted out of the hole that was left when a slab was overturned suggests that they were not clinging to the rock, but were living in the coarse sand under it.

Dead tests were found at stations 17a, 19, 21, 30, and 44; living specimens at station 60.

Genus **MEOMA** Gray

**MEOMA VENTRICOSA** (Lamarck)

Plate 3, figures 4, 5; plate 9, figures 1-4; plate 10, figures 1-4; plate 11 figures 1-6; plate 12, figures 1-4; plate 13, figures 1-3; plate 15, figure 6; plate 16, figures 5, 6; text figures 8-14

This large spatangoid (150 mm. long) has a high brown test covered with relatively short spines. The bare dead test is white and has

only four petals, all of which are approximately equal in length and well depressed below the surface of the test. The tubercles are all small, and the plastron is narrow. This species is distinguished from the other large spatangoid that often occurs with it, *Plagiobrissus grandis*, by its higher heavier test, lack of long spines on the upper surface, more depressed petals, darker color, and wider plastron.

*Growth*.—Two small spatangoids, 22 and 44 mm. long, seemed different from all the other spatangoids known from the Keys. These specimens differ from all other species in the length of their spines, shape of test, arrangement and relative length of the petals, size of peristome, and occurrence of fascioles. After considerable study, however, these specimens were recognized as immature *Meoma ventricosa*, unusual in that the growth changes that normally occur in specimens much smaller than 22 mm. in other spatangoids are postponed in this species. Presumably it is because this species becomes so large that even very young specimens are as large as adults of other species. The young of this species would be large enough to be considered adults if no larger specimens were available. Therefore, to clarify the relationships, these growth changes are described in detail below. This information should make possible a reasonably accurate prediction of the appearance of the young of other large spatangoids.

*Shape*.—The shape of the test changes considerably during growth. As the test increases in size it becomes relatively lower. The height of the smallest specimen (pl. 9, fig. 1), 22 mm. long, is 67 percent of the length, but only 53 percent in a specimen 71 mm. long (pl. 9, fig. 3), and only 50 percent in a specimen 144 mm. long (pl. 9, fig. 4). The ratio of the height to the length does not change, as shown by the fairly straight line in the distribution of points in the scatter diagram (fig. 8). The relative width of the test is constant throughout growth; in the smallest test the width is 87 percent of the length, and in a large specimen it is 88 percent (fig. 8).

The petals are only slightly depressed in the two specimens 22 and 44 mm. long (pl. 9, figs. 1, 2) but in a specimen 71 mm. long (pl. 9, fig. 3) they are considerably depressed, and in a full size specimen, 144 mm. long (pl. 9, fig. 4), they are deeply depressed. Likewise the anterior ambulacral groove is shallow in the smallest specimen, slightly more depressed in a specimen 71 mm. long, and deeply depressed in a large specimen. Because of depression of the ambulacra, the adapical interambulacra appear more inflated in the adults.

The periproct on the smaller specimens is situated high on the posterior truncation, and because this truncation is nearly vertical on

these smaller specimens (pl. 9, fig. 1) the periproctal opening is not visible from the adoral side. The opening is lower on the larger tests and the truncation is tilted so that the opening is partially visible from the adoral side on a specimen 71 mm. long (pl. 9, fig. 3), and completely visible on a full-size adult (pl. 9, fig. 4).

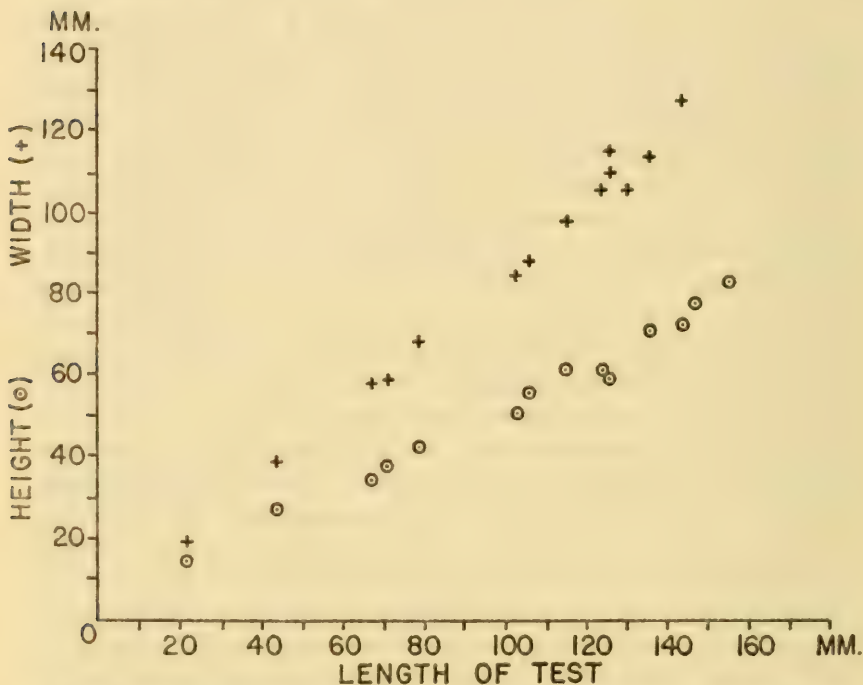


Fig. 8.—*Meoma ventricosa* (Lamarck). Scatter diagram showing rates of increase in height and width of test as length increases.

The dorsal posterior surface of the smallest specimen is highly inflated (pl. 9, fig. 1), but on larger specimens (pl. 9, figs. 3, 4) it is depressed and slopes steeply posteriorly. Anteriorly the situation is reversed, with the front steep in the smallest specimen, but more gently sloping in the larger.

*Petals.*—One of the most striking differences between small and large *Meoma ventricosa* is in the relative length of the posterior petals. In the smallest specimen available (pl. 9, fig. 1), 22 mm. long, the posterior petals extend only one-half the distance from the apical system to the margin, whereas in a specimen 144 mm. long (pl. 9, fig. 4), they extend 83 percent of this distance. A scatter diagram

(fig. 9) of this relative length of the petal to the length of the test illustrates that in specimens up to 65 mm. long the rate of increase in petal length is much greater than in specimens longer than 65 mm. The rate of introduction of new pore-pairs in the petals decreases correspondingly during growth (fig. 10). Between the lengths of 22 mm. and approximately 100 mm. 8-10 new pore-pairs are added for each doubling of the length of the test. For example, a specimen 44

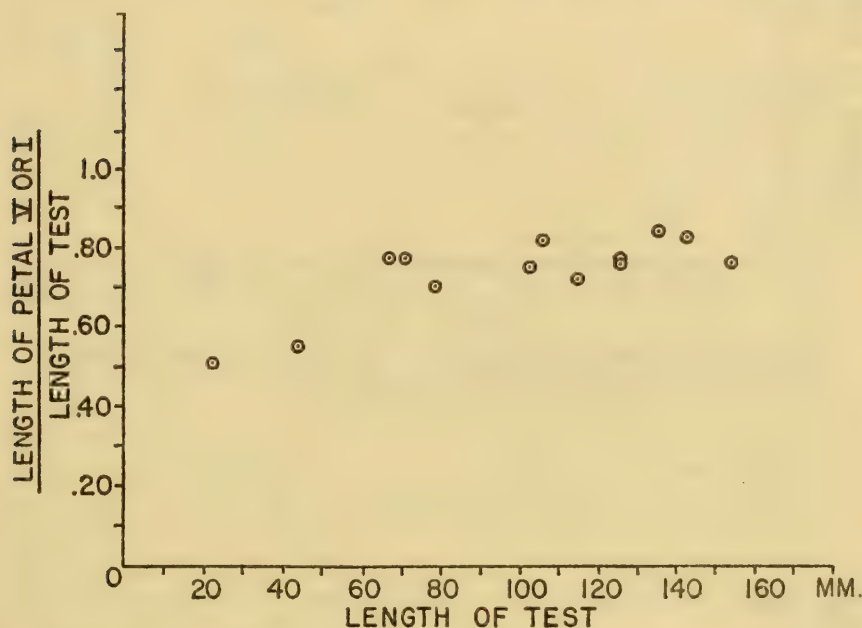


Fig. 9.—*Meoma ventricosa* (Lamarck). Scatter diagram showing proportionate increase in length of petals with increase in size of test. This trend is illustrated in a series of photographs on plate 9.

mm. long has 10 more pore-pairs in a single poriferous zone than a specimen only 22 mm. long. In specimens over 100 mm. long, production of new pore-pairs has almost ceased, with approximately 41 pore-pairs in each poriferous zone of each of the four petals.

The shape of the anterior petals also changes. In the smallest specimen (pl. 9, fig. 1) these petals are straight, but in the larger specimen (pl. 9, fig. 4) their ends curve anteriorly. The posterior petals curve slightly posteriorly in the smaller specimens but slightly anteriorly in the larger. Furthermore, the anterior petals are more divergent in the smaller specimen where they subtend an angle of 162 degrees than



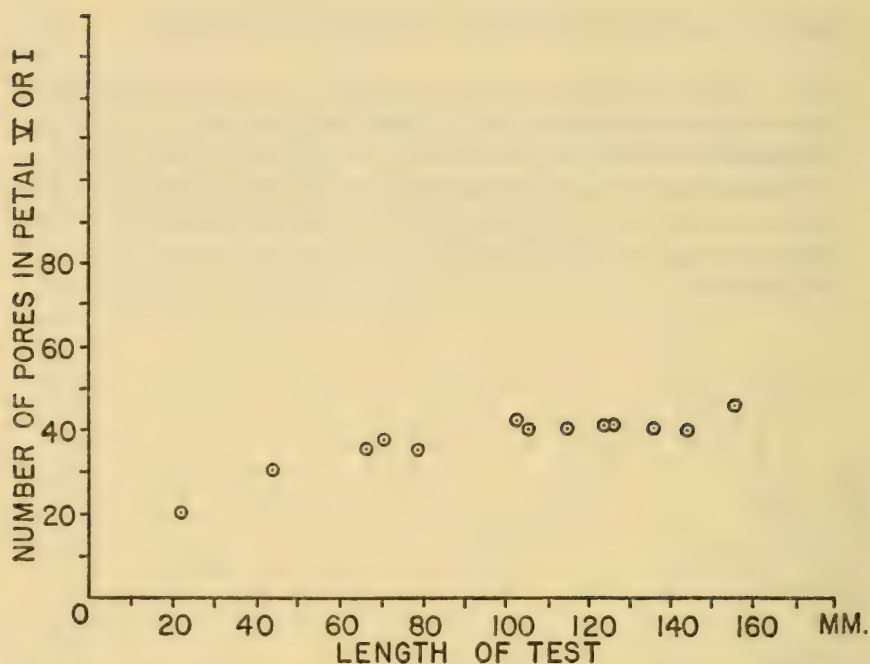


Fig. 10.—*Meoma ventricosa* (Lamarck). Scatter diagram showing increase in number of pores in petals with growth of test.

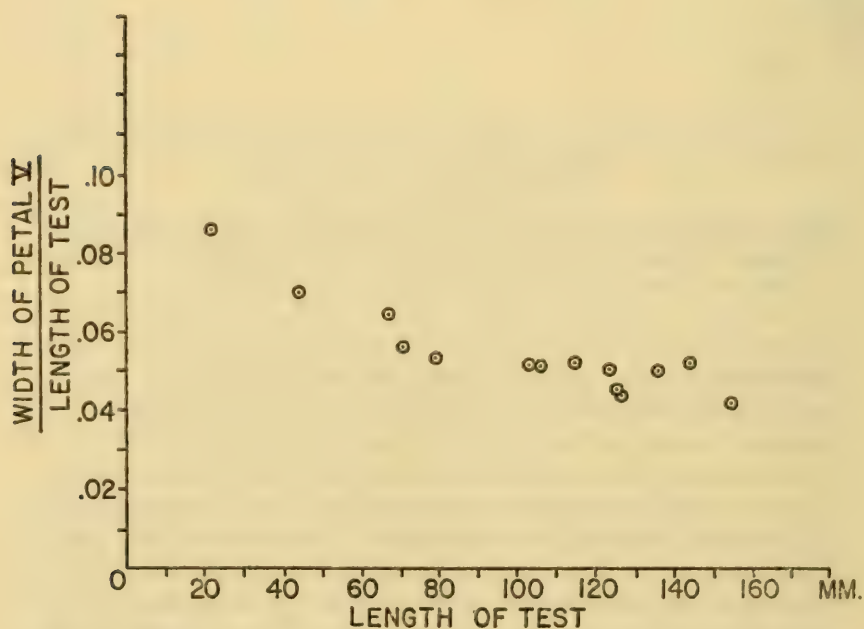


Fig. 11.—*Meoma ventricosa* (Lamarck). Scatter diagram showing proportionate decrease in width of petal V with increase in length of test.

in the larger with an angle of 135 degrees. The posterior petals are less divergent, having an angle of 56 degrees in the smallest specimen as opposed to 65 degrees in a large specimen.

The petals are relatively much wider in the smaller specimens than in the larger (see pl. 9). In the smallest specimen, 22 mm. long, the width of one of the posterior petals is 8.6 percent of the length of the test, but only 5.3 percent in a specimen 79 mm. long and only 4.2 percent in the largest one studied, 155 mm. long. The greatest rate of change (fig. 11) in the width of the petals occurs in the specimens under 80 mm. in length.

*Phyllodes*.—Phyllodes are well developed in the smallest specimen, and do not change significantly during growth except by the addition of pores. In the smallest specimen 6 pores occur in each of the poriferous zones of the anterior paired phyllodes, whereas 9-11 occur there in specimens over 66 mm. long. Presumably these additional pores were produced by enlargement and alteration of the small pores in the ambulacral plates immediately adapical to the phyllodes. The small sensory tubefeet that passed through these small pores must have changed into the pencillate tubefeet found in the phyllodes.

*Peristome*.—The outline of the peristome changes considerably during growth. In the smallest specimen it is proportionately large, with a length 22 percent of the length of the test, whereas in a large specimen its length is only 15 percent of the test length. In the smallest specimen (pl. 9, fig. 1) the peristomal opening is high, but as the echinoid grows the labrum enlarges and extends anteriorly (pl. 9, fig. 3) until in a large specimen (pl. 9, fig. 4) it extends nearly to the anterior margin of the peristome. This development of the labrum is also apparent in the profile views on the same plate.

*Periproct*.—Besides changing its position, as described in the section on shape, the relative size of the periproct changes during the growth of the test. The periproct of the smallest specimen is proportionately larger, with a height 23.8 percent of the length of the test, whereas the periproct of the largest specimen is only 14.2 percent of the test length. A scatter diagram (fig. 12) illustrates that the rate of change in the relative size of the periproct opening is greatest in the smaller specimens, with almost no change in rate in specimens over 100 mm. long.

*Spines*.—The spines are relatively much longer on smaller specimens, particularly spines within the peripetalous fasciole (see pl. 10). One measured spine is 5.1 mm. long in the smallest specimen, or 23 percent of the length of the test, whereas on a large specimen, one

is 7.4 mm. long or only 5 percent of the length of the test. Spines of juveniles, therefore, are more than 4 times as long relative to the size of the test as are spines of large specimens. Similarly, the large adoral spines are proportionately 2.5 times larger on the smallest specimen.

*Fascioles*.—Although the peripetalous fasciole changes little during the growth of the echinoid, the subanal fasciole undergoes a striking change. In the smallest specimen (fig. 13A) that portion of the

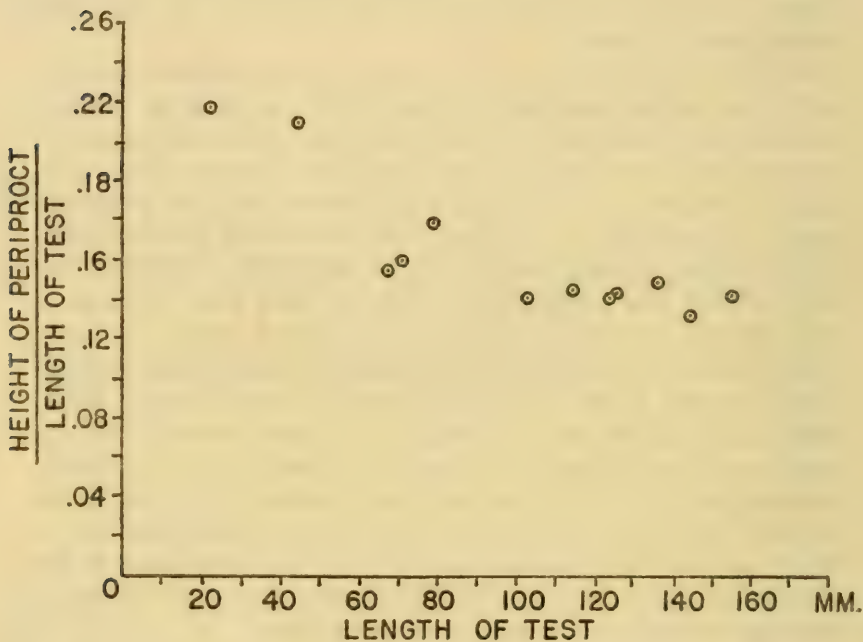


Fig. 12.—Scatter diagram showing proportionate decrease in height of periproct with increase in size of test.

fasciole nearest the periproct is wide, but in a specimen 44 mm. long (fig. 13B) it is much narrower, and finally in a specimen 71 mm. long (fig. 13C) it is completely absent. Mortensen (1951, p. 528) reports the same loss of this portion of the fasciole in *Meoma grandis* Gray.

*Apical system*.—No genital pores are present in the smallest specimen, but in a specimen 44 mm. long (fig. 14A) three very small pores are present, but none in genital plate 2, the madreporite. In the next larger specimen available, 71 mm. long (fig. 14B), the genital pores are fully open and all four are present. In a large specimen 144 mm. long (fig. 14C), the madreporite is greatly expanded posteriorly,

widely separating the posterior oculars. Some madreporitic pores also occur in genital plate 1. Mortensen (1951, p. 529) reports that genital pores appear in *Meoma grandis* Gray when the echinoid is about 50 mm. long.

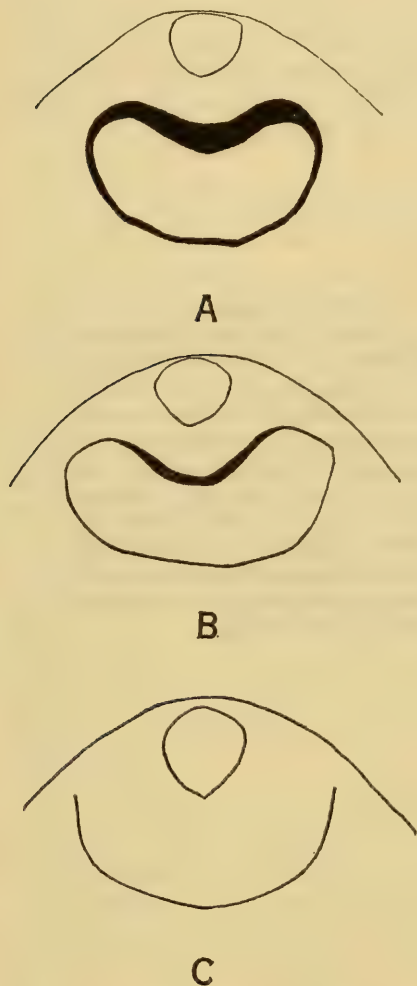


Fig. 13.—Change in subanal fasciole during growth of *Meoma ventricosa* (Lamarck). In the smallest specimen, 22 mm. long, that portion of the fasciole near the periproct is broad but decreases in width during the growth of the echinoid and is absent in an adult. A. USNM E10315; station 19; 22 mm. long;  $\times 3$ ; B. USNM E10314; station 17; 44 mm. long;  $\times 1.7$ ; C. USNM E10313; station 30; 71 mm. long;  $\times 1$ .

In one of the larger specimens, 144 mm. long, the last plates (adapical) in the posterior interambulacrum are not in contact with the posterior oculars. As shown by Kier (1956, p. 971) this separation indicates that production of new interambulacral plates has ceased in this area.



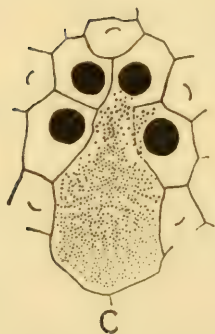
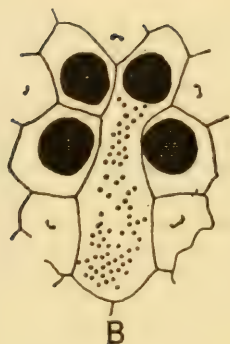
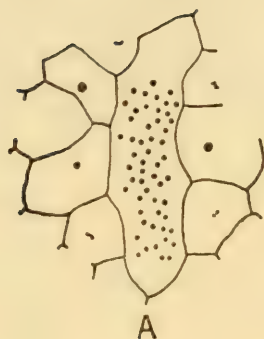


Fig. 14.—Growth changes in the apical system of *Meoma ventricosa* (Lamarck). Only three small genital pores present; A. specimen 44 mm. long ( $\times 16$ ); station 17; USNM E10314. B. Madreporite beginning to expand posteriorly; all genital pores present; specimen 71 mm. long ( $\times 10$ ); station 30; USNM E10313. C. Madreporite greatly expanded posteriorly; specimen 144 mm. long ( $\times 5.3$ ); station 17b; USNM E10312.

*Summary.*—The following changes occur during the growth from 22 mm. in length to full size:

1. Test becomes lower, more angular, petals become depressed, posterior truncation tilts so that periproct is visible adorally.

2. Posterior petals become much longer, all petals become relatively narrower and curved at the ends.

3. The peristome becomes smaller relative to the length of the test, and the labrum enlarges and extends anteriorly.

4. The spines become more equal in size, and proportionately much shorter.

5. The subanal fasciole becomes discontinuous because of the elimination of that portion of the fasciole nearest the periproct.

6. Genital pores are introduced when a specimen is approximately 40-60 mm. long.

Most of these growth changes also occur in *Plagiobrissus grandis* (Gmelin).

*Occurrence.*—*Meoma ventricosa* occurs in sandy areas relatively far from shore. It is most abundant, and reaches its maximum size, in areas of clean sand that are free or nearly free of grass or dense patches of algae. However, specimens somewhat below the normal size were found in turtle grass, along with *Clypeaster rosaceus*. Their range extends from the inshore edge of the White Bank to the sandy terraces offshore from the main reef (and possibly also beyond, outside our area of study). It is most abundant on the White Bank and in the "interreef deep channel," and rare on the deep terraces beyond the reef. The inshore limit of its range overlaps only slightly with the outerlimit of *Lytechinus variegatus*; the two are seldom found together (fig. 5).

The depth range of *M. ventricosus* is between 10 and 85 feet; specimens were not found at 110 feet, but a wider search at that depth might disclose them. The species is most abundant in depths between 20 and 40 feet, and in some areas within that depth range a specimen can be dug up about every two or three feet of traverse. An area 40 feet by 40 feet at station 19, in 40 feet of water produced 40 specimens of *M. ventricosa* in about 20 minutes of searching, during which time only 6 specimens of *Clypeaster subdepressus* were discovered in the same area.

This large and thick species requires rather deep sand for its burrowing, so it was absent from small patches of sand within rocky or reefy areas where a few *C. subdepressus* could survive.

This species was found at stations 17, 17b, 19, 20, 21, 22, 23, 24 (dead), 27, 29, 30, 36 (dead), 37, 39, 44, 45, 49, 51, 52, and 53.

*Behavior.*—*Meoma ventricosa* burrows through the sand with the dorsal surface of the test covered to a depth of as much as 1.5 inches. Most dig less deeply than that, and many keep the uppermost part of dorsal surface nearly at the surface of the sand. These sort the sand slightly, to keep relatively coarse grains and shell fragments over the petal areas, and are visible from above (pl. 11, fig. 6). Some specimens seemed to burrow steadily through the sand, leaving even trails, each with a narrow row of coarse sand in the middle. Others apparently moved more sporadically, leaving trails that consisted of connected series of low mounds marking where individuals repeatedly stopped and again moved forward.

Some specimens were found in areas of dense turtle grass (pl. 3, fig. 4), where the tangled root systems made burrowing impossible. These were smaller than the average adult living in clean sand, and they lived above the surface of the sand covered with shell fragments, sand grains, and a few blades of grass, much in the manner of *Clypeaster rosaceus*, and associated with that species. Blades of turtle grass were preferred for cover by *C. rosaceus* in grassy areas, but in the same areas *M. ventricosa* used mostly sand and coarse sand size shell fragments, and only a few blades of grass (pl. 3, figs. 4, 5).

When excavated and placed on the surface of the sand, *M. ventricosa* buries itself without moving forward. It brings sand laterally away from the ventral surface (pl. 11, figs. 4, 5), and up along the sides, thus displacing the sand and moving the test directly downward into the sand. The displaced sand forms two low, crescent-shaped mounds, one on each side, and these ultimately coalesce over the dorsal surface of the test. However, before they meet, the test is already effectively covered by a thin layer of sand that has been brought up onto the petal area (pl. 11, fig. 5). The process of burial is lengthy, and gradually slowing. The excavated animal is reburied to about half its height in about 7 to 9 minutes, but only about 75 percent covered after 20 minutes. From then the process slows even further, although the test may be effectively covered by the thin layer over the petals after about 30 minutes. The individual is buried to "burrowing depth" after 40 to 50 minutes, and then may begin to move forward. This process is much slower than the reburial of the thin sand dollars *Encope michelini* and *Leodia sexiesperforata*, and also somewhat slower than that of the thicker form, *Clypeaster subdepressus*. It is also much slower than the burial process of the similarly large

but much more active spatangoid *Plagiobrissus grandis*, which can bury itself in a little over 10 minutes.

*Meoma ventricosa* is able to right itself relatively rapidly when overturned. An excavated specimen was placed on the sand on its dorsal surface, along with three specimens of *Clypeaster subdepressus*, two of which are illustrated on plate 6, figures 1-6. The process of righting began at 10:15. By 10:30 *M. ventricosa* had achieved a strong tilt while two of the *C. subdepressus* were barely moved, and one small one slightly tilted. The *M. ventricosa* was nearly on edge by 10:35, but the most rapid *C. subdepressus* (pl. 6, fig. 2) did not attain an angle of 45 degrees until 10:50. The *M. ventricosa* had righted itself by 10:40, in contrast, the most rapid of the *C. subdepressus* did not become completely righted until about 11:15, but then was completely buried and actively burrowing only three minutes later. At that time the slower two *C. subdepressus* nearby had only raised to about 45 degrees, when the observations were terminated.

*Meoma ventricosa* turns over on its anterolateral edge, in a direction similar to that of *C. subdepressus*, and in contrast to the anterior direction of overturning of *Encope michelini* and *Leodia sexiesperforata*. However, it does not dig that edge into the sand as does *C. subdepressus*, but seems merely to "walk" itself over on its spines, while remaining on the surface of the sand.

This species apparently feeds by passing sand through its system and extracting whatever nutrient particles are included. A dissected specimen 144 mm. in length was nearly entirely full of sand; the entire contents of the test had a dry weight of 191 grams. The mouth remains open as the animal moves anteriorly through the sand, the labrum serves as a scoop, and sand is forced into the mouth by the anterior motion of the whole animal.

*Predation.*—*Meoma ventricosa* seems to be rather frequently victimized by the starfish *Oreaster reticulatus* (Linnaeus). One such incident was observed directly (pl. 12, figs. 1, 2). The urchin was unburied, on the surface of the sand, and the starfish was draped over its dorsal surface. When the starfish was lifted off, its extruded gut was seen to retract. The area of the urchin that had been covered by the gut of the star was devoid of spines, and the test was comparatively thin (pl. 13, figs. 1-3) demonstrating local digestive dissolution. As soon as the starfish was removed, the urchin began to move its spines in the normal burrowing or reburying motion, but while the starfish was on it, the urchin did not move. Possibly the starfish secreted some form of mild narcotic agent along with whatever fluids



were dissolving spines and the test of the urchin. Previously, many specimens had been observed with large or small areas that were free of spines, and which, as a consequence, were but poorly covered by sand (pl. 11, figs. 2, 3). Later examination of specimens in the laboratory showed others, each with the spineless area stained a brownish purple where the digestive fluids of the starfish had been active. Apparently *M. ventricosa* is a frequent victim of *O. reticulatus*. Some individuals obviously were able to escape alive, but with some portion of the test stripped of spines.

Several specimens of *M. ventricosa* with bare areas devoid of spines were observed at station 21. These lay buried just below the surface of the sand, and the spineless areas remained uncovered by sand. A small fish, identified by J. E. Randall as the red band parrot fish *Sparisoma aurofrenatum* (Valenciennes), was seen to swim to the urchin and nip at the exposed areas. Some of the specimens were dug up and placed on the surface of the sand, and the parrot fish photographed as it nipped them (pl. 11, fig. 1). The spineless areas in these specimens differ from those in which the spines had been removed by dissolution by *Oreaster reticulatus*. No spines were partly dissolved, or "thinned" as in a second specimen taken from station 23 where the starfish was observed in process of attacking an urchin, and there was no sign of partial dissolution of the test. Furthermore, the depressed petalous areas retained their spines, and only the highly convex areas between petals were denuded. Possibly these are specimens that were attacked by *O. reticulatus*, but made good their escape, with the fish then taking advantage by nipping at the areas that lacked spines and therefore were not covered by sand. However, the difference in the bare areas, cited above, suggests that they were due to the grazing of the fish.

### Family SCHIZASTERIDAE Lambert

#### Genus SCHIZASTER Agassiz

#### Subgenus PARASTER Pomel

#### **SCHIZASTER (PARASTER) FLORIDIENSIS Kier and Grant, new species**

Plate 13, figures 4-6; plate 14, figures 1-9; text figure 15

*Diagnosis*.—Species characterized by central apical system, narrow ambulacrum III, and flexuous anterior petals.

*Material*.—Four denuded tests, one incomplete specimen with spines.

*Measurements.*—

<i>Length</i>	<i>Width</i>	<i>Height</i>
40.0	39.5	27.0
36.9	35.4	28.9
21.6	20.6	17.0
21.1	19.6	16.2

*Shape.*—Test subglobular, nearly as wide as long with greatest width near center, test high, with height 70-80 percent of length; anterior margin indented, posterior slightly truncated, margin slightly angular particularly in larger specimens; in side view anterior profile sloping steeply, posterior nearly vertical, indented at and immediately below periproct; node present on most interambulacral plates on adapical surface, nodes on interambulacral plates where crossed by fasciole; adorally test slightly convex, plastron more convex.

*Apical system.*—Central to slightly posterior to center; depressed below interambulacra; four genital pores (pl. 13, fig. 5), anterior pair much smaller than posterior, circular to slightly elongated into interambulacra; system ethmolytic with madreporite extending considerable distance posterior to posterior oculars, very narrow where passing between posterior genitals; ocular plate of ambulacrum III small, higher than wide, deeply inserted between genitals 2 and 3; other oculars large, approximately equal in size, roughly pentagonal.

*Ambulacra.*—Ambulacrum III deeply depressed with groove extending over ambitus to peristome; adorally, bottom of groove slightly concave, sides sloping, not vertical; adapically sides steep, almost vertical; pore-pairs arranged in simple regular series near edge of ambulacral groove (pl. 13, fig. p); pores oblique with inner pore of each pair more anterior, smaller, and more elongate than outer; pores near apical system very small, increasing in size anteriorly, last 2 or 3 pore-pairs very small; 15 pore-pairs in poriferous zone in specimen 21.1 mm. long, 18 in specimen 40.0 mm. long; pores beyond axis extending longitudinally to ambulacrum III; petals II and IV long, extending  $\frac{4}{5}$  distance from apical system to margin, curved distally with greatest width  $\frac{2}{3}$  distance from apical system to end of petal; both pores of each pair approximately same size, outer pore more slitlike than inner; interporiferous zone narrow, approximately same width as distance between pores of pore-pair; 22 pore-pairs in each poriferous zone in specimen 21.1 mm. long, 26 in specimen 40.0 mm. long; posterior petals V and I short, extending less than  $\frac{1}{2}$  distance from the apical system to the margin, one-half as long as petals II and IV, greatest width near midlength of petal; interporiferous zones approxi-

mately same width as distance between pores of pair ; 14 pore-pairs in poriferous zone of specimen 21.1 mm. long, 19 in specimen 40.0 mm. long ; pores beyond all petals single, slitlike, situated on adoral edge of plate.

*Phyllodes*.—Broad (pl. 13, fig. 4) pores single, large, on adoral edge of oval depression ; three pores in ambulacrum III, 7-8 in ambulacra II and IV, 6-7 in ambulacra V and I.

*Peristome*.—Anterior, located 70 percent anterior of distance between posterior and anterior margins ; opening wide, low, crescent shaped.

*Spines*.—Preserved only on one incomplete small specimen (pl. 14, figs. 4, 5), originally approximately 23 mm. long ; adapically most of specimen missing, spines expanded at tips, spines near ambulacra curving over ambulacra ; adorally, plastron spines (pl. 14, fig. 9) very distinct, long, 4.5 mm. long, flattened and expanded at tips transverse to length of test, tips curving anteriorly, similar spines but longer (6 mm. long) on edge of posterior interambulacra adjacent to ambulacra V, I ; no long spines in phyllodes or most of posterior ambulacra ; few minute spines, 0.5 mm. long, scattered over otherwise bare surface ; long tapering, pointed tipped spines (6 mm. long) in anterior interambulacra and a few in ambulacrum III.

*Sphaeridia*.—Many sphaeridia present along full length of posterior ambulacra on adoral side ; a few in phyllodes of the other three ambulacra.

*Periproct*.—Longitudinal, high on posterior truncation.

*Tuberculation*.—Adapically, tubercles inside and outside of peripetalous fasciole of approximately same size ; adorally tubercles on plastron situated anteriorly on raised oval platforms, centrally in other areas ; peripetalous and lateroanal fascioles present ; peripetalous fasciole passing close to extremities of petals, (pl. 14, fig. 3), curving sharply inward in all interambulacra except interambulacrum 5, fasciole widest at extremity of petals II and IV (anterior paired petals), narrowest at indentations in interambulacra ; lateroanal fasciole leaving peripetalous fasciole in posterior paired interambulacra and passing down under periproct ; narrowest at peripetalous fasciole, greatest width directly under periproct.

*Pedicellariae*.—(Fig. 15). Only two pedicellariae found on single specimen with spines, both globiferous (pl. 14, figs. 6-8 ; text fig. 15) with valves, 0.4 mm. in length ; base of valve relatively broad, tapering to slender, tubular blade above apophyses ; two lateral articulating teeth present on articular face, just above the median apophysis rises



vertically one-third length of valve, then angles back to join lower portion of tubular blade; valves in contact distally only at terminal teeth; two terminal teeth of each valve forming horizontal fork; each valve containing internal poison chamber. Small terminal opening between teeth.

*Internal calcareous process.*—Support on interambulacrum 4 narrow, erect, almost vertical, sloping slightly sideways and posteriorly.

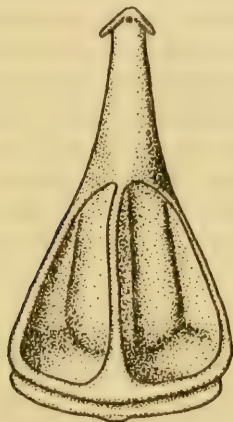


Fig. 15.—*Schizaster (Paraster) floridiensis*. Valve of pedicellaria from figured paratype USNM E10303;  $\times 94$ .

*Comparison with other species.*—This species is easily distinguished from the three living species of the subgenus *Schizaster (Paraster)*. It differs from *S. (Paraster) gibberulus* (L. Agassiz) from the Red Sea and Indian Ocean in its more anterior apical system, more flexuous anterior petals, narrower ambulacrum III, and lack of transverse ridges in ambulacrum III. It is distinguished from *S. (Paraster) compactus* Koehler from the Bay of Bengal by having the pores in the anterior ambulacrum oblique to each other, a wider higher test, shorter wider posterior petals, and more divergent anterior paired petals. It differs from *S. (Paraster) rotundatus* Doderlein, a Pacific species, in having a more anterior apical system, its posterior petals not extending as near to the posterior margin, and in having more divergent and more flexuous anterior petals.

*S. (Paraster) floridiensis* is distinguished from the West Indian species *Schizaster orbignyianus* Agassiz by its more central apical sys-



tem with four instead of two genital pores, higher, wider test, wider paired petals, more divergent anterior paired petals, and wider peristome. It differs from the Late Pleistocene *S. (Paraster) eustatii* Engel (1961, p. 3) from St. Eustatius in the West Indies by its more anterior apical system, narrower ambulacrum III, and more flexuous anterior petals.

*Type*.—Holotype USNM E10302.

*Occurrence*.—This rare species was not found alive in its habitat. Dead tests were found near the reef in about 35 feet of water (station 19), well beyond the reef on a sandy terrace in 80 feet of water (station 17a), and landward of the reef on sandy bottom in only 15 feet depth at station 30. Probably it lives buried beneath rocks or clumps of sponge and coral, in a manner similar to that of *Brissus unicolor* and *Echinoneus cyclostomus*, and therefore is rarely encountered.

Kier found a dead test of the same species on a sandy bottom at 85 feet depth off the southern Caribbean island of Dominica. Because the species has never been taken alive, its habitat preferences remain unknown.

#### ENEMIES OF ECHINOIDS

No general survey of the predator-prey relationships of echinoids is intended here, but our observations of victimization of echinoids by other animals are significant enough to warrant emphasis. The most incontrovertible attack observed was that by the starfish *Oreaster reticulatus* upon *Meoma ventricosa*, as described above in the discussion of that species (pl. 12, figs. 1, 2). To our knowledge, this is the first record that *O. reticulatus* may feed upon *M. ventricosa*. This urchin also is attacked by the red band parrot fish (*Sparisoma aurofrenatum*) which nibbles away spines on the dorsal surface that are not completely protected by a cover of sand (pl. 11, fig. 1).

Other examples of fish predation were noted when specimens of the thin sand dollars *Encope michelini* and *Leodia sexiesperforata* were overturned to see how they right themselves. When the urchins were nearly vertical, in the process of righting themselves, a little burrowing fish nipped at the upturned edges. Many injured specimens of these thin sand dollars were seen, some with nearly one-quarter of the test broken away, but nevertheless healed and bearing spines. Undoubtedly this breakage could have resulted from several causes, one of which may be biting by fish.

Predation of *Plagiobrissus grandis* by species of the helmet conch *Cassis* has been noted above in the discussion of that species. One observation led us to believe that *Cassis* preys upon other species of echinoids as well. A specimen of *Clypeaster subdepressus* at station 57 on sand in 18 feet of water was crushed as though it had been stepped upon by a heavy foot. About 6 feet away, on the surface of the sand, was a live specimen of *Cassis madagascariensis* Lamarck about 7 inches long. Possibly the large gastropod had eaten the urchin, and had broken up the test by action of its foot, which was about the same diameter as the echinoid. If this happened, it contrasts strongly with the manner in which *C. madagascariensis* drills into the fragile test of *P. grandis* by means of its radula, leaving the test unbroken, and only the small circular drill-hole as evidence of its predation. However, that process occurs beneath the surface of the sand, with both the gastropod and the victim remaining buried. The *C. subdepressus* was on the surface, near where it normally lives, and the *Cassis* shell was smooth and clean of encrusting algae except for an area of about 4 square inches on its highest dorsal elevation, indicating that it was out of its normal buried habitat. Until this type of predation by *Cassis* is actually observed, it must be regarded merely as an inference from circumstantial evidence.

Dead tests of the small burrowing spatangoid *Brissus unicolor* also had the small circular hole that indicates predation by a gastropod. As *C. madagascariensis* is an efficient burrower, and a known predator of burrowing echinoids, possibly it also feeds upon *B. unicolor*.

Several dead tests of *Clypeaster subdepressus* were collected, in which the ventral surface was almost completely excavated, and the remaining rim marked by numerous short radiating scratches (pl. 15, fig. 8). The organism that preyed upon the urchin was not observed, but presumably it was a fish.

#### RELATION OF TEST SHAPE TO LIVING HABIT

Thin discoid species such as *Leodia sexiesperforata* and *Encope michelini* normally inhabit the upper part of the sand substrate. They burrow to a depth of only about a quarter of an inch under normal circumstances, although in some areas they were found slightly deeper. Hyman (1955, p. 556) cites studies that indicate that sand dollars dig deeper in stormy weather. The thicker and less completely flattened *Clypeaster subdepressus* also lives very near the surface of the

sand, and some specimens were observed to cover themselves with a layer of sand and carry it with them as they move over the surface without burrowing. This species has the flat ventral surface that characterizes species that burrow.

The other common *Clypeaster* in the Coral Reef Preserve is *C. rosaceus* which we did not find buried, and whose shape is greatly different from that of *C. subdepressus*. The test is strongly convex dorsally, a feature in common with burrowing spatangoids, but the oral surface is deeply concave, a shape not found in burrowers. The concavity of the oral surface keeps the nearly centrally located mouth raised somewhat above the sand as the animal moves over the surface. This shape would be an impediment to motion in a burrowing species, but probably is advantageous to *C. rosaceus* in allowing the test to ride over tufts of grass, and then to fill the concave underside as the animal stops to feed.

Thick or tumid forms such as *Meoma ventricosa* and *Plagiobrissus grandis* are somewhat streamlined and have the ventral surface flat. This shape is efficient for burrowing deeper than do the flat sand dollars, and size probably is no impediment to motion, providing the thickness of sand is sufficient.

All the regular echinoids we saw lived above the surface of the sand. Some such as *Echinometra lucunter* may live in deep niches in rock. We noted no preferred direction of motion of active regulars such as *Lytechinus variegatus* or *Tripneustes ventricosus*, an observation corroborated by Hyman (1955, p. 550) who reports that *L. variegatus* can walk with any ray forward, and cites Parker (1936) to the effect that the axis of forward motion frequently changes as the animal progresses.

Sand dwelling regular echinoids live above its surface, and some like *Astropyga magnifica* (and the presumably nocturnal *Diadema antillarum*) are surprisingly mobile.

#### ABNORMAL SPECIMENS

One tetramerous variant of *Meoma ventricosa* was found alive at locality 23. This specimen (pl. 16, figs. 5-6) lacks ambulacrum IV (left anterior) and its two associated half-interambulacra. Ocular IV and genital 3 are missing from the apical system. This variant is typical of the tetramerous variant group 4 as described by Jackson (1927, p. 502). Because only four ambulacra are present at the peristome (where the oldest, first-produced plates occur), it is apparent



that this abnormality dates from a stage before any skeletal parts had formed. With ocular IV absent, no plates could be introduced for ambulacrum IV and its two adjacent half-interambulacra for as shown by Jackson (1912, p. 26; 1927, p. 491) new plates are introduced at the edges of the ocular plates. This prospective gap was filled by the joining of the anterior half of interambulacrum 3 with the posterior half of interambulacrum 4. Ambulacrum III which is normally anterior shifted to the side of the test with its phyllode entering the side of the peristome instead of the front (pl. 16, fig. 6). The calcareous process that normally occurs in the interior at the edge of the peristome, attached to the first plate of interambulacrum 4, also is absent because that plate is missing. It is significant that the echinoid was able to live without this process. We have been able to find little in the literature concerning this structure, but from our study of dissected specimens of *Meoma ventricosa*, and as figured in the *Traité de Zoologie* (Grasse, 1948, vol. 11 p. 157, fig. 183) in *Spatangus purpureus* Müller, the esophagus is attached to this process by numerous mesenteries. Presumably this process keeps the esophagus from being pushed posteriorly by motion of sand through it as the echinoid moves anteriorly.

One tetramerous variant of *Encope michelini* also is referable to Jackson's group 4; it lacks ambulacrum IV and the two associated half-ambulacra. In this specimen (pl. 15, fig. 7) the anterior petal is shifted to the left. Because only four ambulacra occur at the peristome, and the lantern consists of only four jaws, teeth, and other parts, this abnormality also predates the development of any skeletal parts.

In contrast to the previous two variants, which are probably mutational, one specimen of *Echinometra lucunter* is incompletely tetramerous, probably because of post-embryonic injury. Adapically (pl. 16, fig. 2), only four ambulacra and four interambulacra are present, with ambulacrum I and its associated half-interambulacra missing. Adorally (pl. 16, fig. 1), all five ambulacra and five interambulacra are present but ambulacrum I and its half-interambulacra (pl. 16, fig. 4) terminate a short distance from the peristome and their place is filled by interambulacral plates from oculars V and II. The lantern is normal with five components of each structure, and there are five auricles. Apparently, therefore, the production of plates for ambulacrum I and its half-interambulacra ceased when the echinoid was small and had produced only a few plates in each column. This cessa-



tion could have been caused by an injury near ocular I where new plates are produced. The posterior genital plates, 5 and 1, have no pores, but two large pores in ocular I presumably are the pores normally found in those genital plates (pl. 16, fig. 3).

### CONCLUSIONS

Echinoids studied here seem to show definite habitat preferences that could provide significant clues to interpretation of conditions in ancient seas by paleoecologists. Moreover, they could be valuable to the modern ecologist or sedimentologist who retrieves samples by dredge or trawl. For example, *Clypeaster rosaceus* dredged from clean sand would indicate that grassy areas were nearby, as grassy sand is the preferred habitat of that species. In addition, the material that this species carries on its back is a clear indication of the nature of the bottom. Similarly, the paleoecologist who found a fossil of this species or a species of similar shape, such as *Clypeaster antillarum* Cotteau from the Tertiary of the Caribbean area, could infer the presence of turtle grass on the former sea bottom. This in turn gives an indication of limits of depth at which the Tertiary formation was deposited, because this grass does not thrive much below 40 feet.

Many of the species that live in the Coral Reef Preserve occur as fossils, and others have near relatives that are known from Tertiary and Quaternary formations. A fossil assemblage that contains *Lytechinus variegatus*, with *Arbacia punctulata* (or similar *A. improcera* (Conrad)) and *Eucidaris tribuloides* or a similar form, indicates a sandy bottom with dense turtle grass, at depths as great as 40 feet, but relatively near shore. Admixtures of *Clypeaster subdepressus*, or the similar fossil *C. sunnilandensis* Kier, and some of the thin sand dollars indicate patches of clean, grassless sand among the turtle grass.

*Meoma ventricosa* has not been reported as a fossil. However, species similar to it in shape, such *Rhyncholampas evergladensis* (Mansfield) which occurs in the Tamiami Formation of Florida (Kier, 1963), probably had similar living habits. These forms indicate a sandy bottom with little or no turtle grass, located relatively far from shore. Likewise, a sandy, grassless bottom could be inferred from presence of *M. ventricosa* or similar forms in a dredge haul.

Some species of regular echinoids seek rocky or reefy environments, where niches and rock slabs provide cover. All large *Diadema antillarum* observed in the Coral Reef Preserve were on rocky sub-

strate, only small and medium-size individuals were congregated in groups on the sand. Therefore, a fossil assemblage consisting of large *D. antillarum*, along with *Echinometra viridis* and perhaps *Eucidaris tribuloides*, would suggest a hard substrate, possibly a reef or rocky shore. *Echinometra lucunter*, on the other hand, lives only in the intertidal zone, so its presence would suggest either a shoreline environment, or a shoal.

*Factors controlling echinoid distribution.*—Three major factors seem to control the distribution of the echinoid species in the area studied. These are depth, substrate, and distance from shore. Other possible influences, such as light penetration, wave agitation, current direction, water temperature, and food supply, either are functions of the three major factors, or were influences which we were unable to evaluate.

*Species controlled by depth.*—*Echinometra lucunter* inhabits rock just below low tide, whether along the shore of Key Largo, or on exposed parts of the reef several miles from shore. Although it inhabits rocky substrates, it is absent from rocks at depths greater than about 10 feet.

Species that inhabit turtle grass are controlled indirectly by the depth of water. Turtle grass does not survive at depths greater than about 40 feet; *Lytechinus variegatus*, *Tripneustes ventricosus*, and *Clypeaster rosaceus* seem to be confined to waters shallower than that depth. Turbidity seems not to have had great influence, as these species were found in clear water as well as in the extremely murky waters of Hawk Channel.

*Astropyga magnifica* was found only deeper than 75 feet. Its distribution may depend on other factors, such as the nature of the substrate, but depth also seems to be a major factor.

*Species controlled by substrate.*—The sand dwellers, *Encope michelini*, *Leodia sexiesperforata*, *Clypeaster subdepressus*, *Meoma ventricosa*, and *Plagiobrissus grandis* are confined by their necessity to burrow. They must have relatively grassless sand, where they are unobstructed by the tangle of roots. The few specimens of *M. ventricosa* found in turtle grass were unable to burrow, and were living on the surface of the substrate, covered by objects they held onto the test in the manner of *Clypeaster rosaceus*.

*Brissus unicolor* and *Echinoneus cyclostomus* were found only under detached pieces of rock in areas of coarse sand, and perhaps their distribution is confined to such areas. However, too few specimens were observed to be sure of this relationship.

Species whose distribution is controlled by the distribution of turtle grass might be said to depend on substrate, but as depth controls the turtle grass, it also indirectly controls the echinoids.

*Species controlled by distance from shore.*—*Meoma ventricosa* inhabits waters of greatly varying depth, but was not encountered nearer than about 4 miles from shore, just a short distance landward from the reef. Although it was found in shallow water on White Bank, it was not found in deeper water nearer shore.

*Species not evaluated.*—Factors controlling the distribution of *Diadema antillarum* could not be evaluated within the area studied. The species was found in all depths, on all substrates and its range extends from shore to the seaward limit of the area.

The habitat of *Echinometra viridis* is not well enough known to evaluate factors controlling its distribution. At present it seems to inhabit only niches in rock, and the shadows of sponge and coral heads, in the manner of *Arbacia punctulata*. Furthermore, its depth tolerances are unknown.

*Echinoid associations.*—Certain echinoid species characteristically occur near one another as inhabitants of similar or contiguous environments. Five such associations were encountered in the area studied.

1. *Echinometra lucunter* and *E. viridis* live in holes in rock near shore, and under the shadows of corals and sponges in shallow water just offshore.

2. *Lytechinus variegatus*, *Tripneustes ventricosus*, *Clypeaster rosaceus* and *Eucidaris tribuloides* live above the surface of the sand in turtle grass. In addition, *Arbacia punctulata* and *Eucidaris tribuloides* cluster around isolated mounds of coral or sponge within these grassy areas. *Diadema antillarum* also inhabits the turtle grass, with adults assembled into groups, and juveniles living singly.

3. *Clypeaster subdepressus*, *Encope michelini* and *Leodia sexiesperforata* inhabit the upper layer of clean grassless sand, and frequently are found together. *Meoma ventricosa* and *Plagiobrissus grandis* inhabit the same areas, although they burrow more deeply. *Clypeaster rosaceus* also may be encountered on the same grassless sand, but normally only where grassy patches occur in the vicinity.

4. *Diadema antillarum* appeared to be nearly the sole inhabitant of niches within the main body of the reef, although one specimen of *Echinometra viridis* was found in a hole in the reef.

5. *Brissus unicolor* and *Echinoneus cyclostomus* live under detached rocks in sandy patches within the reef area.



Further study in other areas of the Caribbean is necessary to test the consistency of these associations, establish other such associations of different species, and to assess their significance as ecological indicators. When a sufficient body of such associational information has been assembled, it should be of value of paleoecologists in interpreting past environments.

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## EXPLANATION OF PLATES

### PLATE 1. *ASTROPYGA MAGNIFICA* IN ITS HABITAT

- 1-5. *Astropyga magnifica* Clark at station 36 (depth 85 feet) on flat sand terrace.
  1. Oblique view of specimen with spines grouped in defensive posture; inflated anal sac visible.
  2. Nearly vertical view from above, dorsal spines bundled for defense, anal sac visible, iridescent spots along ambulacra apparent.
  3. Two specimens showing bundled spines, anal sacs, and iridescent spots; glove at top gives scale.
  4. Small fish (*Apogon*) which characteristically swims among spines of this species.
  5. Same individuals as figure 3, seen from side with black glove in background, showing bundled upper spines, inflated anal sac, iridescent spots, color-banding of spines.

### PLATE 2. HABITATS OF *EUCIDARIS TRIBULOIDES*, *DIADEMA ANTILLARUM*, AND *ARBACIA PUNCTULATA*

- 1-3. *Eucidaris tribuloides* (Lamarck).
  1. Station 36 (depth 85 feet) in niche between boulders.
  2. Station 28 (depth 22 feet) in dense turtle grass.
  3. Station 22 (depth 30 feet) on sand in sparse turtle grass.
- 4-7. *Diadema antillarum* Phillipi.
  4. Station 28 (depth 22 feet) flock of medium size specimens on fine sand in sparse turtle grass. One in bottom center of photograph shows inflated anal sac; small striped fish swim among spines in upper right.
  5. Station 22 (depth 30 feet) solitary juvenile with banded spines on sand in moderately dense turtle grass.
  6. Station 25 (depth 110 feet) large specimen in niche in living coral bank.
  7. Station 60 (depth 20 feet) medium size specimens in niches among living coral on reef.
- 8-9. *Arbacia punctulata* (Lamarck).
  8. Station 28 (depth 22 feet) clinging to base of isolated sponge on sand in sparse turtle grass. White specks are small mysid shrimps which inhabit area protected by spines of this species and *D. antillarum*.
  9. Station 28 (depth 22 feet) two specimens clinging to base of small clump of corals and sponges, on sand in sparse grass.

### PLATE 3. HABITATS OF *LYTECHINUS VARIEGATUS*, *TRIPNEUSTES VENTRICOSUS*, AND *MEOMA VENTRICOSA*

1. *Lytechinus variegatus* (Lamarck) station 28 (depth 22 feet), specimen in turtle grass completely camouflaged by shells and blades of grass held onto test by tube feet.

2. *Tripneustes ventricosus* (Lamarck) station 44 (depth 10 feet), on sand in sparse turtle grass, with a few blades of grass held onto test; typically much less completely covered than *L. variegatus*.
3. Eroded bank about 1.5 feet high, showing exposed roots of turtle grass at station 30 (depth 15 feet). The tangled mat of roots prevents echinoids from burrowing in grassy areas.
4. *Meoma ventricosa* (Lamarck) station 21 (depth 25 feet), two specimens in turtle grass where their normal habit of burrowing is impossible, hence they are covered by sand grains, except along the petals, in a manner similar to *Clypeaster rosaceus*.
5. *Meoma ventricosa* in sand at station 29 (depth 25 feet) living on the surface in the manner of *C. rosaceus*, partly covered by grains of sand and blades of grass; a rare habitat for this species.

#### PLATE 4. CAMOUFLAGED *CLYPEASTER ROSACEUS*

##### 1-7. *Clypeaster rosaceus* (Linnaeus).

1. Station 22 (depth 30 feet), on sand near edge of grass, holding grass and coarse sand on test.
2. Station 30 (depth 15 feet), far from grass, on coarse sand bottom, holding coarse sand grains, shells and shell debris, and worm tubes onto test.
3. Station 21 (depth 25 feet), in sparse grass, covered by shell fragments, coarse sand grains, and a few blades of grass.
4. Station 29 (depth 25 feet), on coarse sandy bottom, covered with sand and shells including dead test of *Brisus unicolor*.
5. Station 20 (depth 35 feet), on clean, fine- to medium-grained sand, partly covered by sand grains, standing immediately to right of faint outline of buried specimen of *C. subdepressus*.
6. Station 29 (depth 25 feet), in dense grass, covered almost exclusively by blades of grass.
7. Station 21 (depth 25 feet), in coarse sand near grassy patch, test sparsely covered by coarse sand grains and grass, moving by plowing through sand rather than by normal habit of moving on surface.

#### PLATE 5. MODE OF BURIAL OF *CLYPEASTER SUBDEPRESSUS*, AND TRAIL OF *ENCOPE MICHELINI*

##### 1-6, 8. *Clypeaster subdepressus* (Gray)

1. Excavated specimen at station 20 (depth 35 feet) begins to rebury itself by passing sand onto the dorsal surface at the anterior, and by moving forward slightly.
- 2-4. Forward motion away from knife blade is apparent; sand is passed onto dorsal surface at ends of petals 3 and 4 as well as being passed backward from the anterior.
5. Burial is complete as specimen has moved forward about one length.
- 6, 8. Specimen at station 49 (depth 20 feet) buries with minimal forward motion, completing burial in about 4 minutes by passing sand onto dorsal surface along petalous areas.

7. *Encope michelini* Agassiz. Station 30 (depth 15 feet). Roughly triangular trail in calcareous sand, showing low parallel ridges made by posterolateral notches, and median row of sand grains aligned by posterior lunule; specimen at top center of photograph.

PLATE 6. OVERTURNING, HABITATS AND ASSOCIATES OF  
*CLYPEASTER SUBDEPRESSUS*

- 1-6. Station 22 (depth 30 feet), timed series illustrating righting of *C. subdepressus* after being overturned.
1. Time 10:30. Small and large specimens overturned, begin righting by action of spines along edge near anterolateral ambulacrum.
  2. Time 10:50. Small specimen at angle near 45 degrees; larger one barely raised (subsequent illustrations show only the smaller specimen; at end of series 45 minutes later, larger specimen still had not attained vertical position).
  3. Time 11:04. Small specimen (at left in figure 2) nearly vertical, with right side dug into sand.
  4. Time 11:10. Small specimen vertical.
  5. Time 11:13. Small specimen rapidly lowering to normal horizontal position.
  6. Time 11:18. Specimen horizontal and buried, beginning to move forward.
7. *Clypeaster subdepressus* and *C. rosaceus*, station 30 (depth 15 feet). Both somewhat out of normal habitat, with tests covered. *C. subdepressus* here moving on surface of sand, with coarse particles held over petal area (this species normally burrows in topmost layer of sand). *C. rosaceus* covered by shells and some grass (this species normally lives in grassy areas).
8. *Clypeaster subdepressus*, station 22 (depth 30 feet), plowing through topmost layer of sand, with broad flat objects held over petals.
- 9-10. *Clypeaster subdepressus* and *Encope michelini*, station 30, depth 15 feet.
9. Two specimens of *C. subdepressus* and one of *E. michelini* covered by thin layer of sand, occupying essentially the same habitats.
  10. The same three specimens uncovered.

PLATE 7. OVERTURNING OF *ENCOPE MICHELINI*, AND BURIAL  
OF *E. MICHELINI* AND *LEODIA SEXIESPERFORATA*

- 1-5. *Encope michelini* Agassiz, station 30 (depth 15 feet).
1. Inverted specimen digs anterior edge into sand.
  2. Side view showing specimen about 45 degrees to surface of sand.
  3. Specimen nearly vertical, without having dug deeper into sand than in figure 2.
  4. Righted specimen lowers posterior edge toward sand.
  5. Nearly horizontal, specimen buries itself rapidly by passing sand backward along dorsal surface, and by moving forward into sand.
- 6-8. *E. michelini* and *Leodia sexiesperforata* (Leske), station 30 (depth 15 feet).
6. Excavated specimen of each species begins to bury by moving forward into sand, passing sand backward along dorsal surface from anterior, and



by passing sand up through notches and lunules (time: 2:31). Both species started at watch band.

7. Both specimens have achieved nearly the same proportion of cover, but *E. michelini* has moved farther forward (time 2:34).

8. Both nearly buried; *E. michelini* moved forward about one length, (time: 2:35).

#### PLATE 8. *PLAGIOBRISsus GRANDIS* BURYING

- 1-4. Timed series illustrating manner and speed by which excavated specimen of *Plagiobrissus grandis* (Gmelin) buries itself, station 30 (depth 15 feet).
  1. Time 3:09. Sand beginning to form ridge around specimen; process began about 1 minute earlier.
  2. Time 3:10. Specimen buried to nearly half its own thickness, pushing up large rim of displaced sand.
  3. Time 3:12. Upper surface of specimen at level of surface of sand; sand from rim being drawn onto test.
  4. Time 3:15. Test nearly covered, long dorsal spines projecting through sand.
5. Partly buried specimen at station 30 (depth 15 feet), showing long dorsal spines.
6. Side view of partly buried specimen at station 23 (depth 12 feet) showing backward curvature of long dorsal spines; rim of displaced sand destroying small ripple.

#### PLATE 9. GROWTH SERIES IN *MEOMA VENTRICOSA*

- 1-4. Specimens showing change in test shape, length and arrangement of petals, size of peristome, and size of tubercles during growth.
  1. Specimen 22 mm. long ( $\times 2$ ); station 19; USNM E10315.
  2. Specimen 44 mm. long ( $\times 1$ ); station 17; USNM E10314.
  3. Specimen 71 mm. long ( $\times 0.6$ ); station 30; USNM E10313.
  4. Specimen 144 mm. long ( $\times 0.3$ ); station 17b; USNM E10312.

#### PLATE 10. *MEOMA VENTRICOSA*

- 1-4. *Meoma ventricosa* (Lamarck)
  - 1, 2, 3. Adapical, adoral, right side of immature specimen, 22 mm. long, showing spines ( $\times 2.5$ ); station 19; USNM E10315.
  4. Adoral view of adult showing difference in length of spines from immature specimen ( $\times 2.6$ ); station 17b; USNM E10312.
5. *Arbacia punctulata* (Lamarck). Station 27; USNM E10320. Adapical view of naked test ( $\times 1\frac{1}{2}$ ).
6. *Echinometra viridis* Agassiz. Station 3; USNM E10319. Adapical view of dried specimen ( $\times 1$ ).

#### PLATE 11. *MEOMA VENTRICOSA* IN SAND

- 1-6. *Meoma ventricosa* (Lamarck) burrowing in sandy bottoms.
  1. Partly buried specimen with depressed petal area being nipped by small parrot fish (*Sparisoma aurofrenatum*). Others nearby with dorsal

spines missing. Shallow sand at station 21 (depth of water 25 feet) at edge of sandy area prevents *M. ventricosa* from burrowing deeply enough to protect themselves.

2. Specimen at station 21 (depth 25 feet) with spines missing near petals, preventing complete burial.

3. Specimen at station 21 (depth 25 feet) with spines missing on posterior lateral surface, preventing complete cover by sand, thus inviting further predation.

4-5. Station 22 (30 feet), timed pair of photographs, indicating speed of burial.

4. Time 10:20. Specimen buried to ends of petals.

5. Time 10:30. Sand being brought up onto test before specimen has burrowed deeply enough for complete burial.

6. Station 18. Normal specimen in normal habitat, showing manner of leaving petals uncovered (or covered only by coarse particles) to allow free circulation of water for respiration.

PLATE 12. *OREASTER RETICULATUS* PREYING ON  
*MEOMA VENTRICOSA*

1. As first observed, station 23 (depth 12 feet), *Oreaster reticulatus* (Linnaeus) draped over an immobile specimen of *Meoma ventricosa* (Lamarck).
2. As the starfish was lifted off the urchin, its extruded gut was seen to contract back into its mouth, whereupon normal burrowing action of the urchin's spines began. Effects on *M. ventricosa* of this predation by the starfish are shown on plate 13.

PLATE 13. *MEOMA VENTRICOSA* AND *SCHIZASTER (PARASTER)*  
*FLORIDIENSIS*

- 1-3. *Meoma ventricosa* (Lamarck). Station 23; USNM E10309.

1, 2. Adapical, rear view of specimen attacked by starfish (see pl. 12, figs. 1, 2). Note black stain on anterior half of adapical surface ( $\times \frac{1}{2}$ ).

3. View of posterior of same specimen showing etching of plates by secretions of the starfish ( $\times 1$ ).

- 4-6. *Schizaster (Paraster) floridiensis* Kier and Grant, new species.

4. View of peristome and phyllodes of holotype ( $\times 3$ ); Station 30; USNM E10302.

5. Apical system of paratype ( $\times 17$ ); Station 30; USNM E10303.

6. Ambulacrum III of holotype ( $\times 6$ ).

PLATE 14. *SCHIZASTER (PARASTER) FLORIDIENSIS*

- 1-9. *Schizaster (Paraster) floridiensis* Kier and Grant, new species.

1, 2, 3. Left side, adoral, adapical view of holotype ( $\times 1$ ); station 30; USNM E10302.

4, 5. Left side, adoral view of paratype with spines ( $\times 2$ ); station 17a; USNM E10303.

6, 7, 8. Globiferous pedicellaria from specimen in figures 4, 5 ( $\times 50$ ).

9. Enlarged view of plastron spines of specimen in figures 4, 5 ( $\times 18$ ).

## PLATE 15. SIX SPECIES OF FLORIDA ECHINOIDS

1. *Echinoneus cyclostomus* Leske. Station 60; USNM E10318. Adapical view of specimen photographed in alcohol ( $\times 2$ ).
- 2-3. *Plagiobrissus grandis* (Gmelin). Station 30.
  2. Adapical view of immature specimen (35 mm. long) for comparison with adult in figure 3 ( $\times 1.5$ ); USNM E 10304.
  3. Adapical view of adult (140 mm. long),  $\times 2.8$ ; USNM E10305.
- 4-5. *Brissus unicolor* (Leske).
  4. Adapical view of specimen photographed in alcohol ( $\times 2$ ); station 60; USNM E10317.
  5. Adapical view of denuded test ( $\times 1.5$ ); station 17a; USNM E10316.
6. *Meoma ventricosa* (Lamarck). Station 23. Pedicellaria clasping an ostracod ( $\times 30$ ).
7. *Encope michelini* Agassiz. Station 45; USNM E10308. Tetramerous variant lacking ambulacrum IV and its associated half-interambulacra ( $\times 1$ ).
8. *Clypeaster subdepressus* (Gray). Station 61; USNM E10307. Adoral view of specimen presumably attacked by a fish as evidenced by the teeth marks on the test. ( $\times \frac{1}{2}$ ).

## PLATE 16. ABNORMAL ECHINOIDS—TETRAMEROUS VARIANTS

- 1-4. *Echinometra lucunter* (Linnaeus). Molasses Key; USNM E10306.
  1. Adoral view showing five ambulacra, five interambulacra, but with ambulacrum I and its half-interambulacra terminating a short distance from peristome ( $\times 1\frac{1}{2}$ ).
  2. Adapical view showing only four ambulacra and interambulacra ( $\times 1\frac{1}{2}$ ).
  3. Apical system showing absence of pores in posterior genital plates, presence of two probable genital pores in ocular I ( $\times 5$ ).
  4. Enlarged view showing total extent of ambulacrum I ( $\times 5$ ).
- 5-6. *Meoma ventricosa* (Lamarck). Station 23; USNM E10311.
  5. Adapical view showing only three petals, the left anterior petal absent ( $\times 0.6$ ).
  6. Adoral view showing absence of phyllode IV ( $\times 0.6$ ).



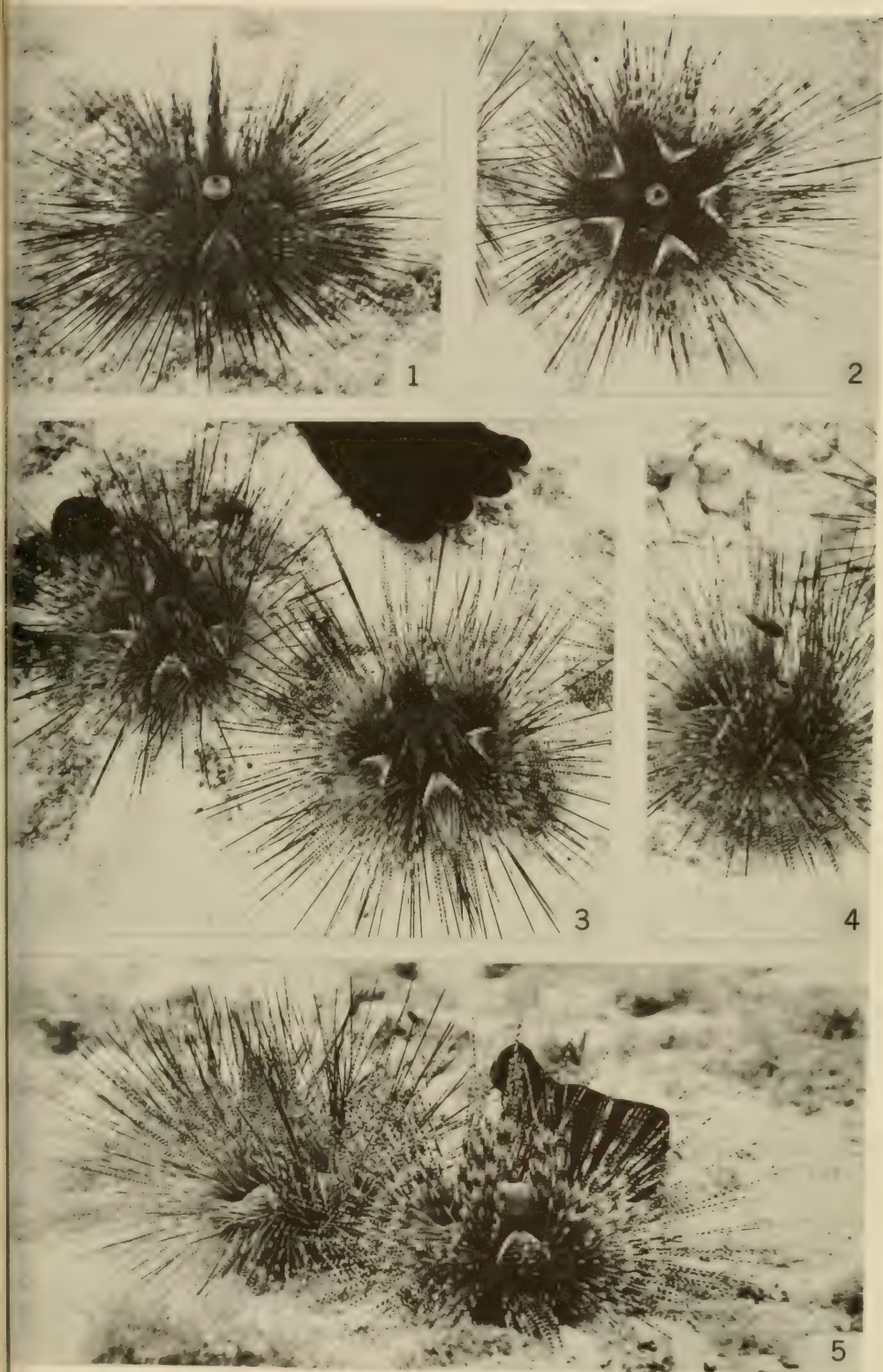


PLATE 1. *Astropyga magnifica* in its Habitat  
(See explanation of plate at end of text.)



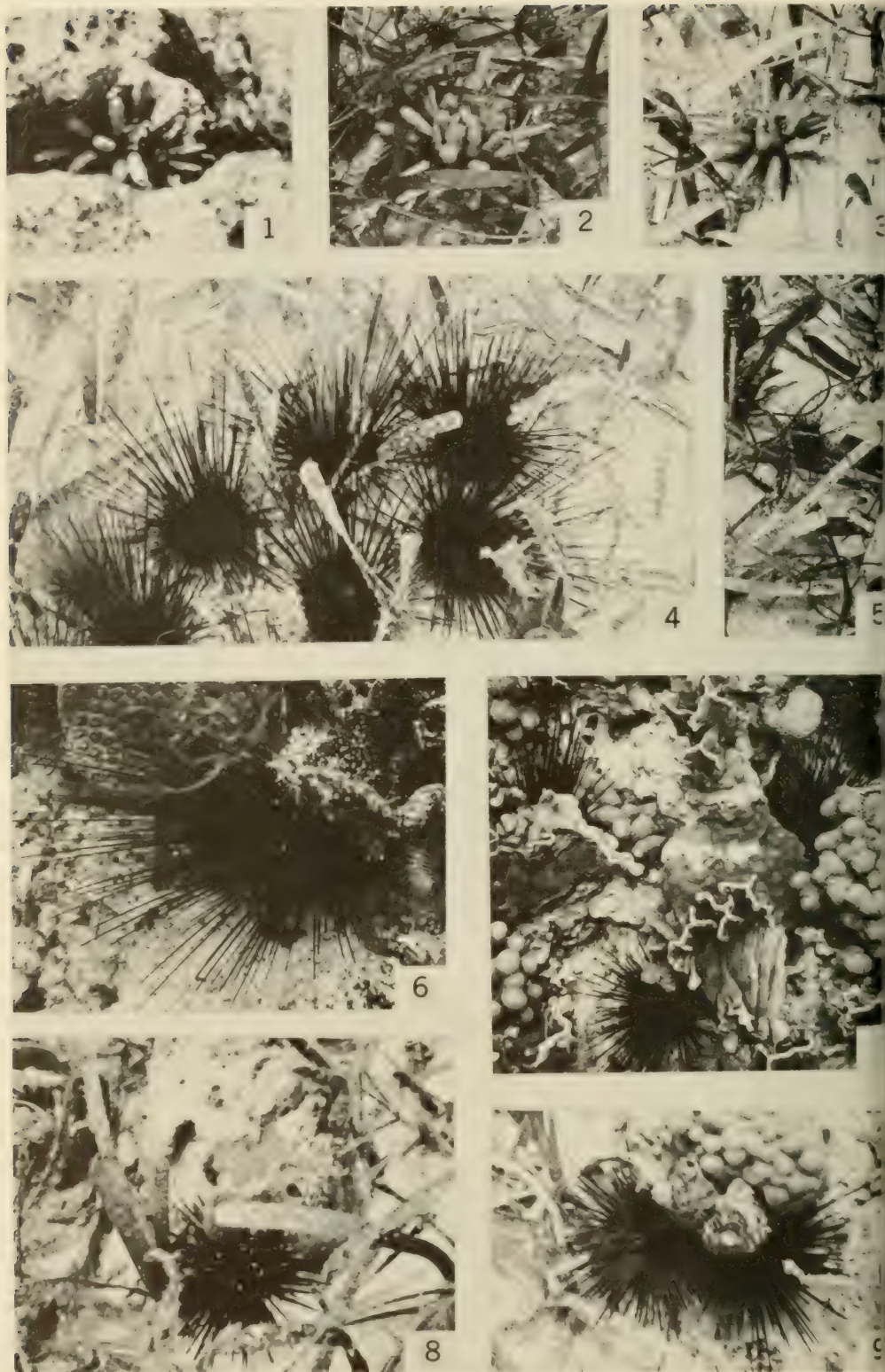
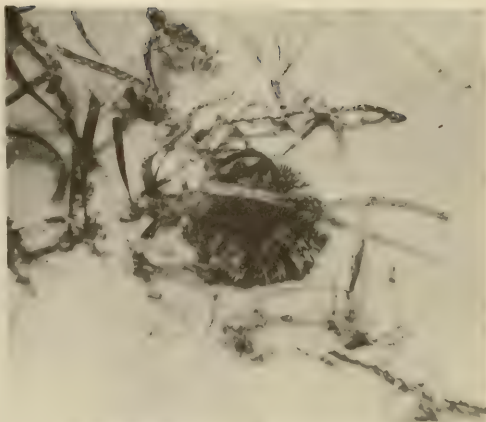


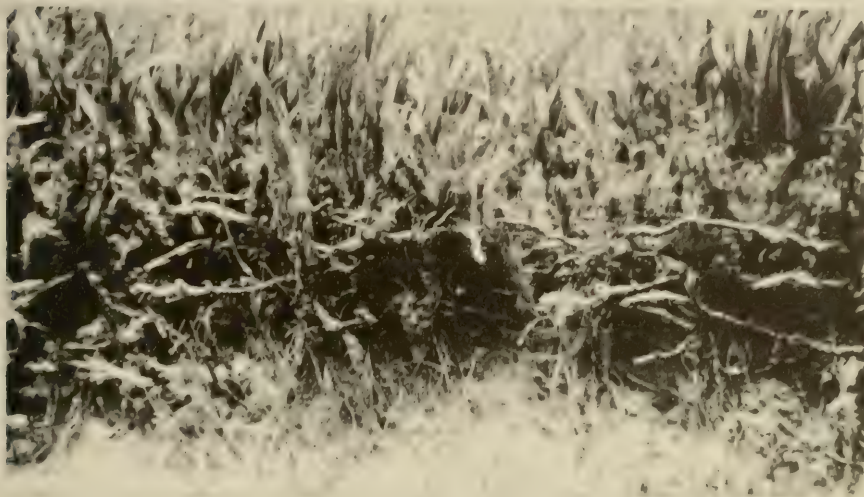
PLATE 2. Habitats of *Eucidaris tribuloides*, *Diadema antillarum*, and *Arbacia punctulata*  
(See explanation of plate at end of text.)



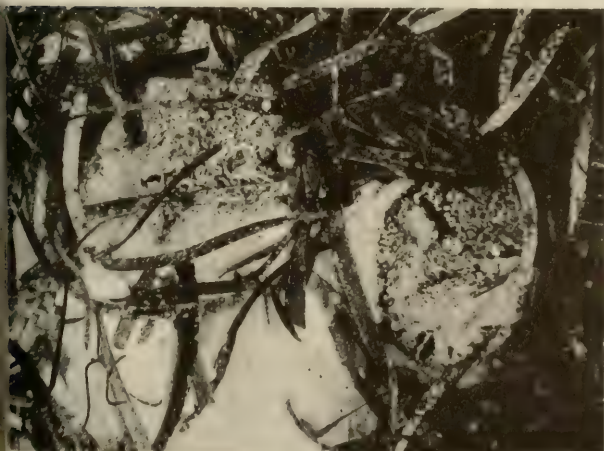
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PLATE 3. Habitats of *Lytechinus variegatus*, *Tripneustes ventricosus*, and *Meoma ventricosa*  
(See explanation of plate at end of text.)



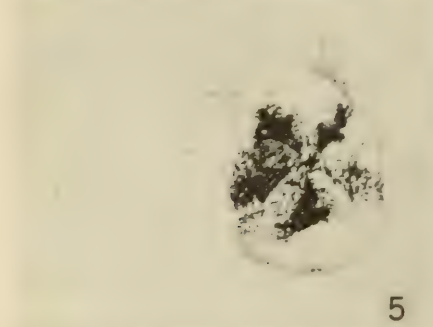
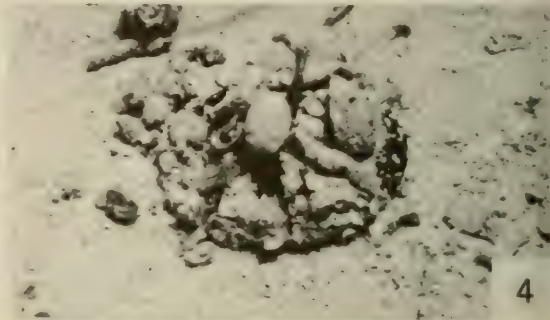
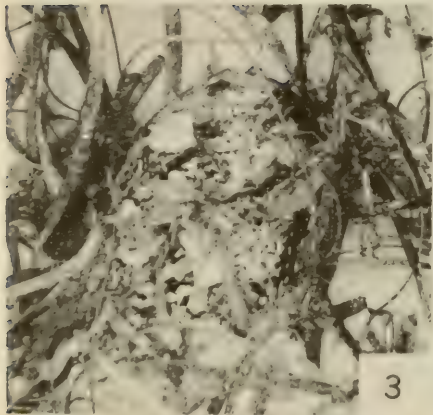
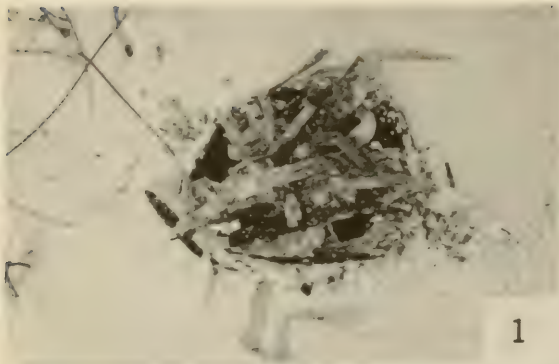


PLATE 4. Camouflaged *Clypeaster rosaceus*  
(See explanation of plate at end of text.)

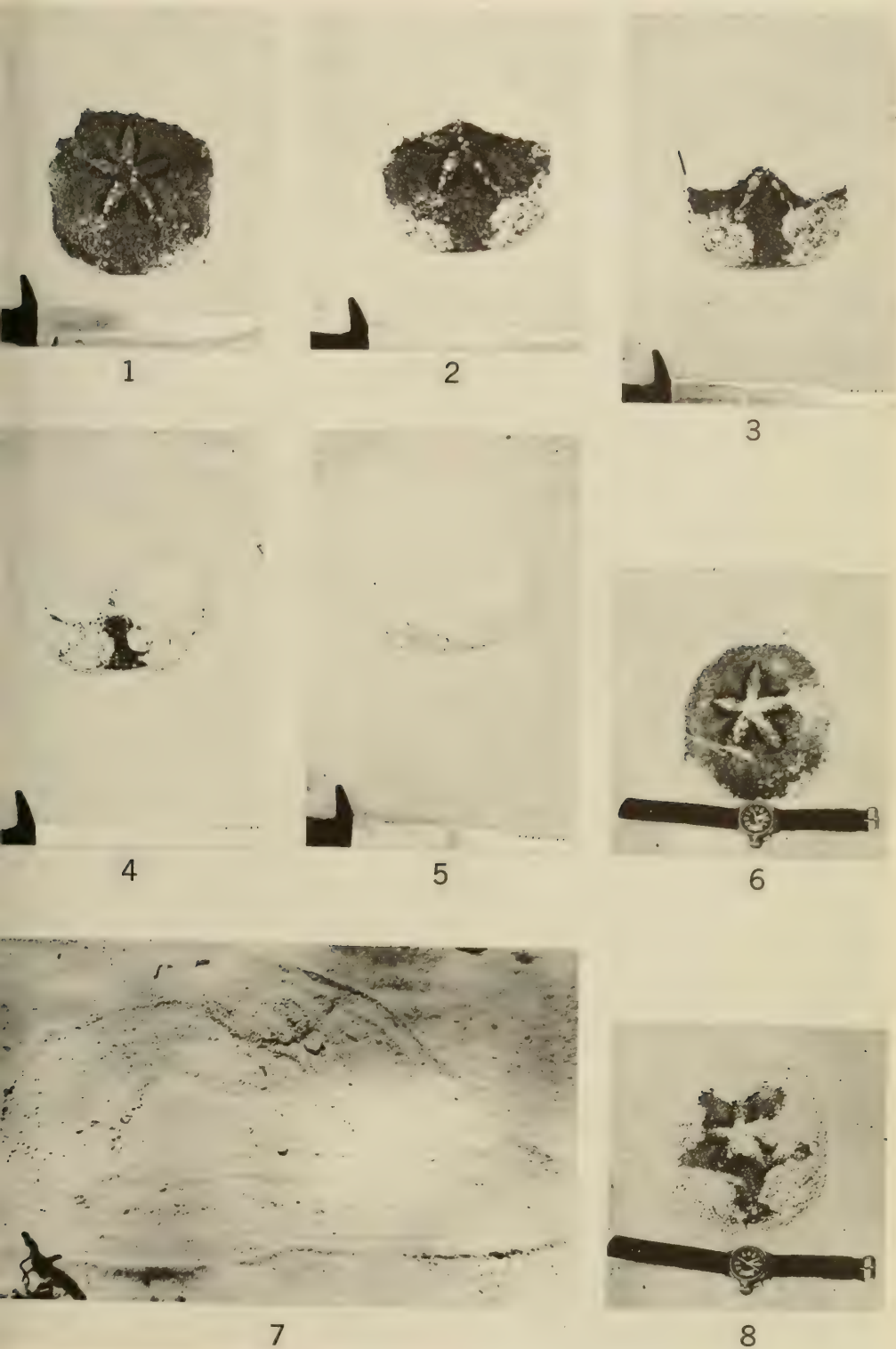
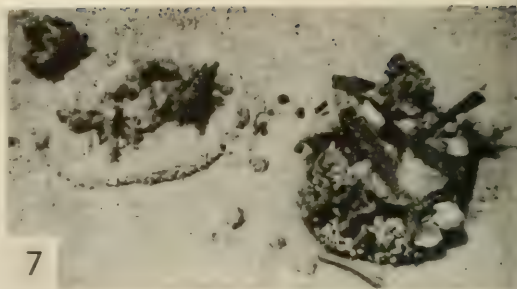


PLATE 5. Mode of Burial of *Clypeaster subdepressus*, and Trail of *Encope michelini*  
(See explanation of plate at end of text.)





10

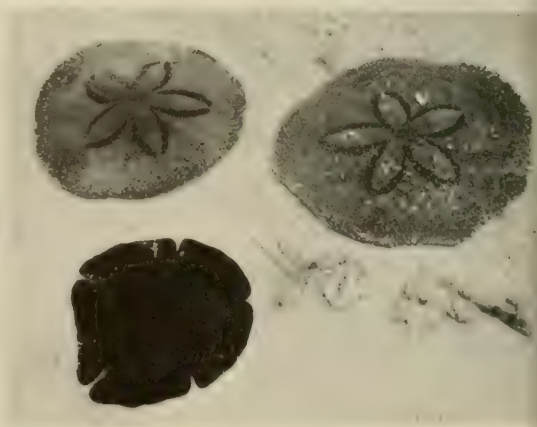


PLATE 6. Overturning, Habitats, and Associates of *Clypeaster subdepressus*  
(See explanation of plate at end of text.)



PLATE 7. Overturning of *Encope michelini*, and Burial of *E. michelini* and *Leodia sexiesperforata*  
(See explanation of plate at end of text.)

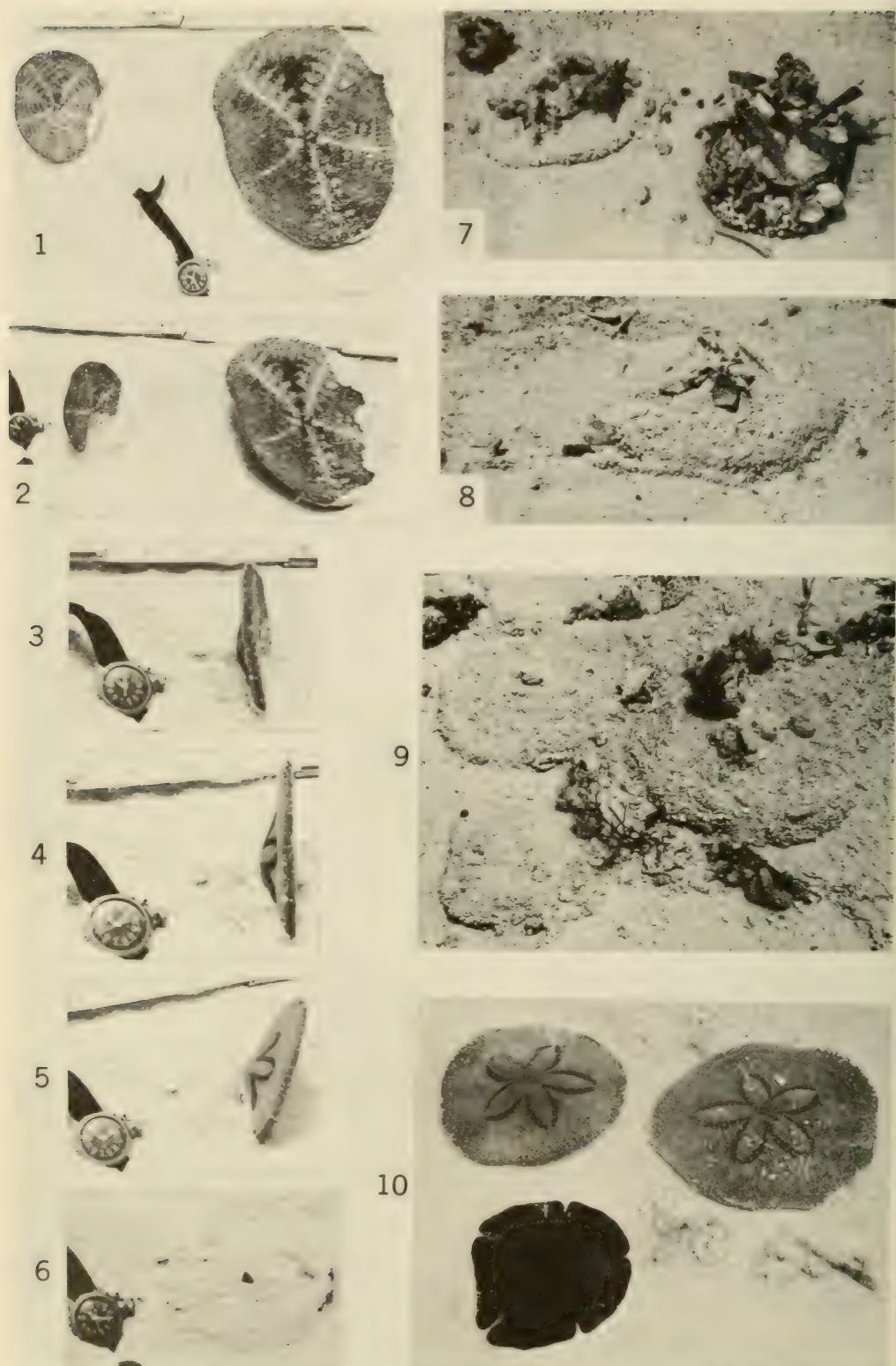


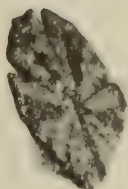
PLATE 6. Overturning, Habitats, and Associates of *Clypeaster subdepressus*  
(See explanation of plate at end of text.)



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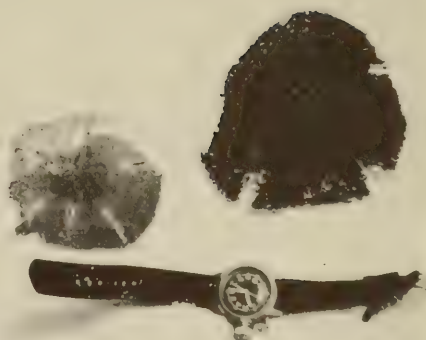
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PLATE 7. Overturning of *Encospe michelini*, and Burial of *E. michelini* and *Leodia sexiesperforata*  
(See explanation of plate at end of text.)



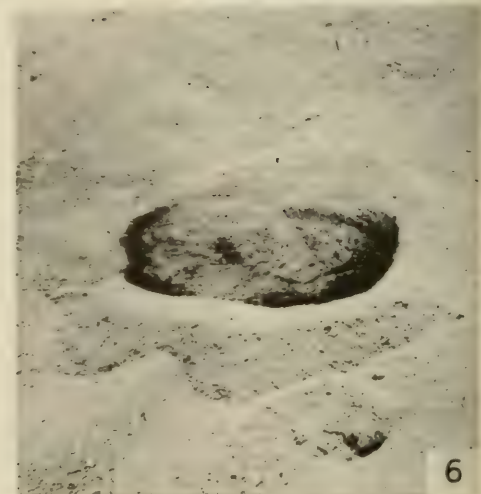


PLATE 8. *Plagiobrissus grandis* Burying  
(See explanation of plate at end of text.)

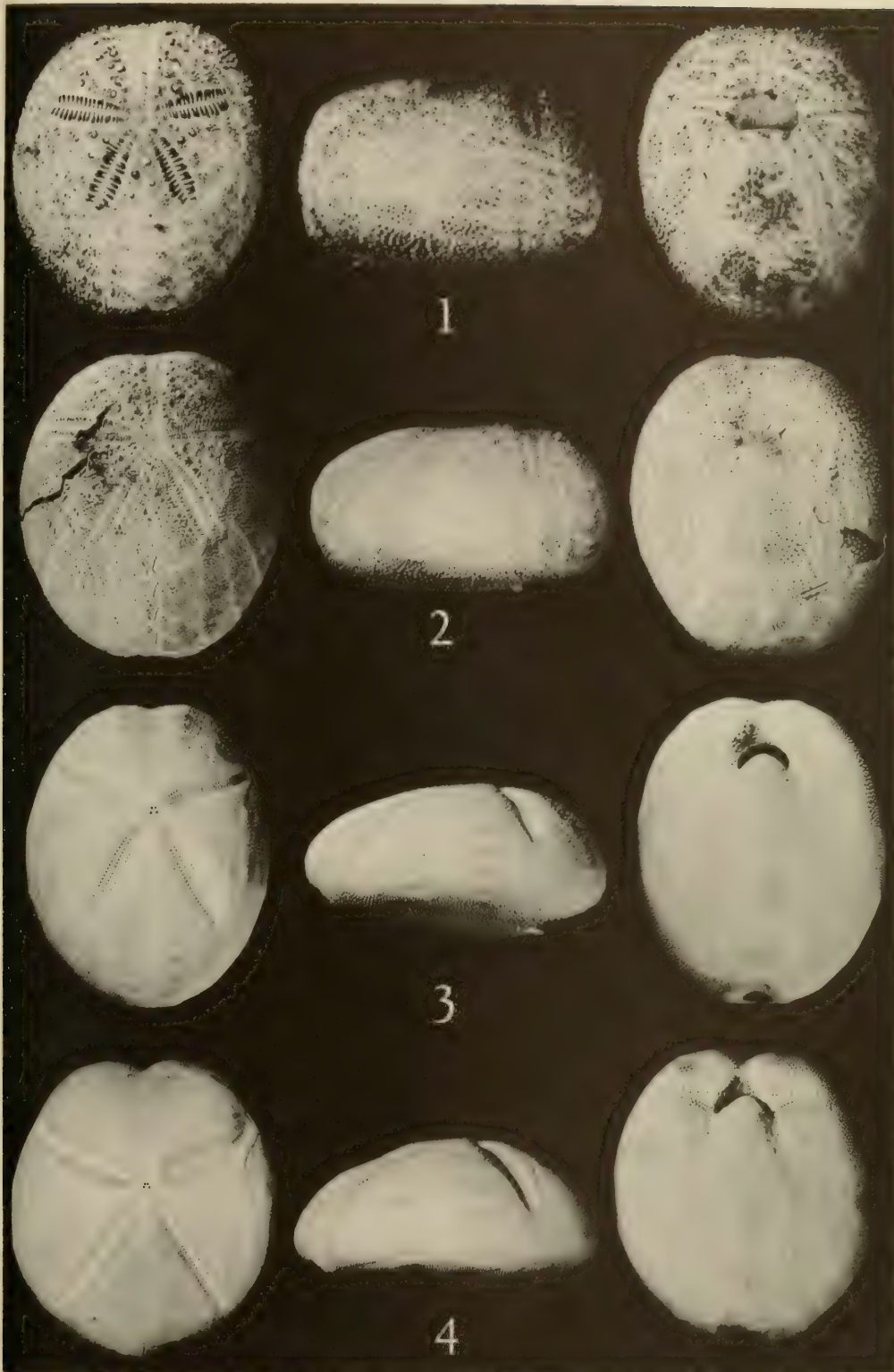


PLATE 9. Growth Series in *Meoma ventricosa*  
(See explanation of plate at end of text.)

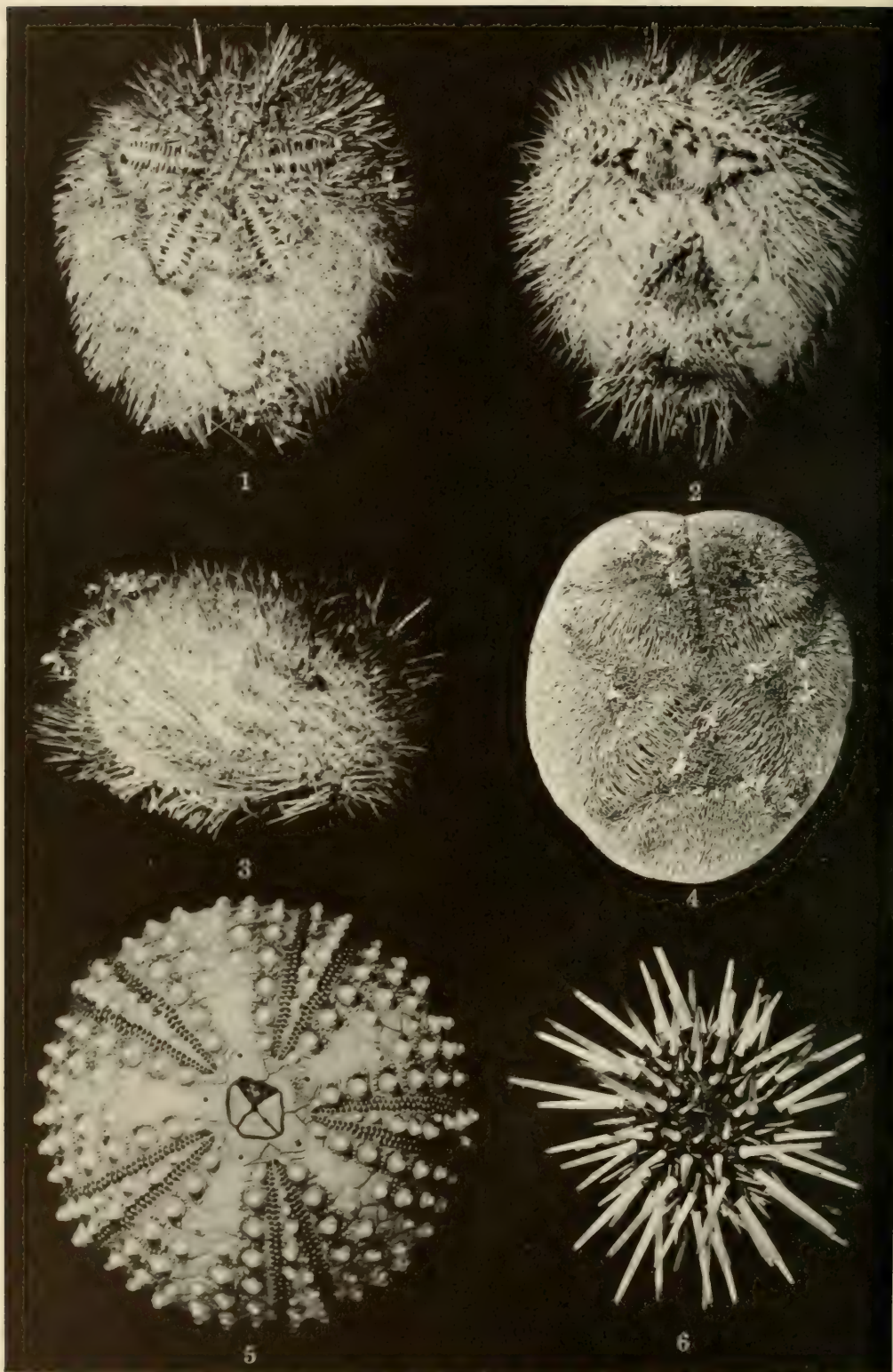
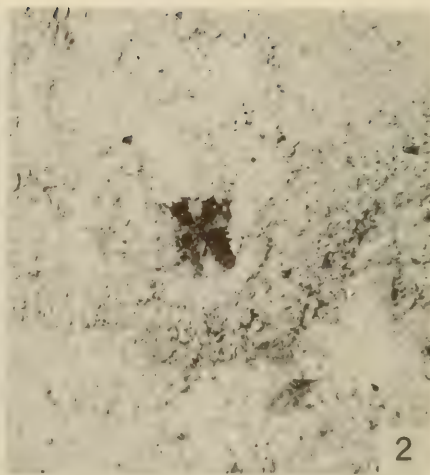


PLATE 10. *Meoma ventricosa*  
(See explanation of plate at end of text.)

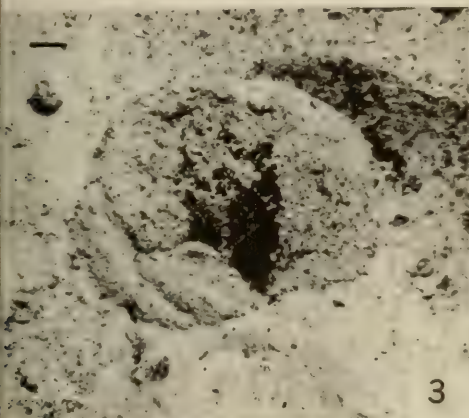




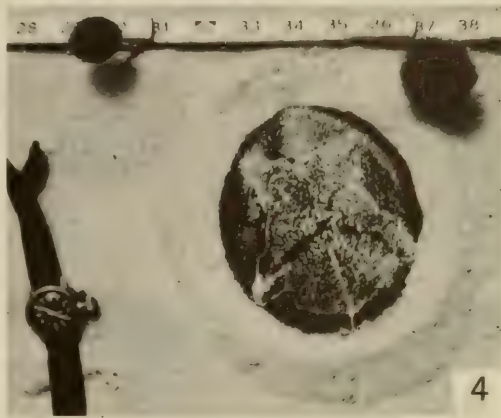
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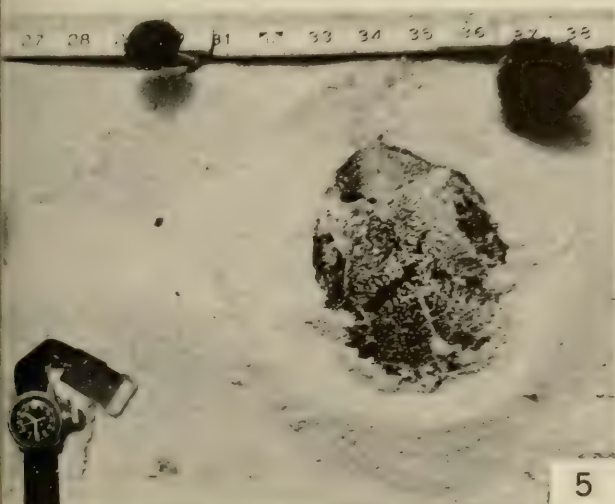
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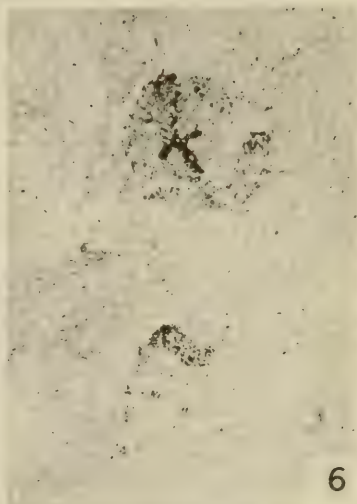
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PLATE 11. *Meoma ventricosa* in Sand  
(See explanation of plate at end of text.)





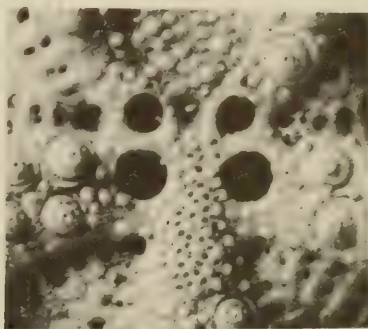
PLATE 12. *Oreaster reticulatus* Preying on *Meoma ventricosa*  
(See explanation of plate at end of text.)



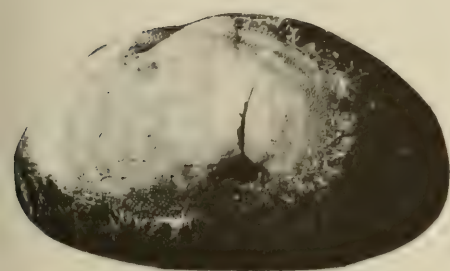
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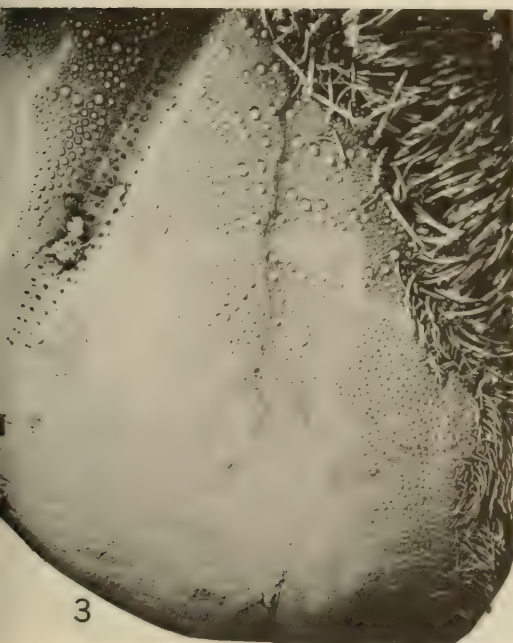
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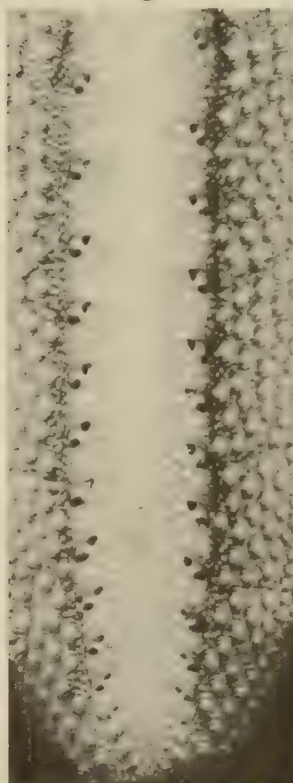
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PLATE 13. *Meoma ventricosa* and *Schizaster (Paraster) floridiensis*  
(See explanation of plate at end of text.)



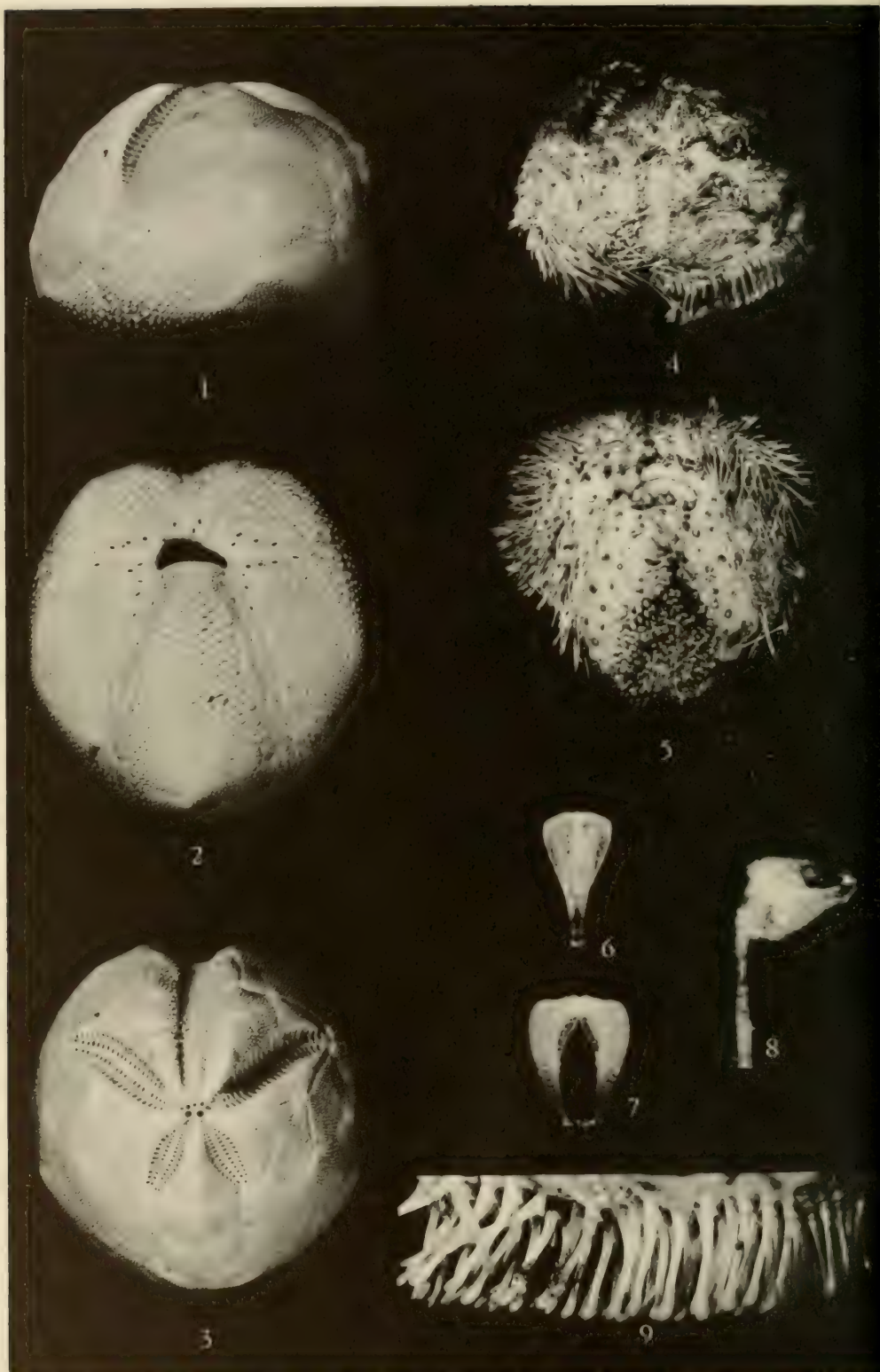


PLATE 14. *Schizaster (Paraster) floridiensis*  
(See explanation of plate at end of text.)

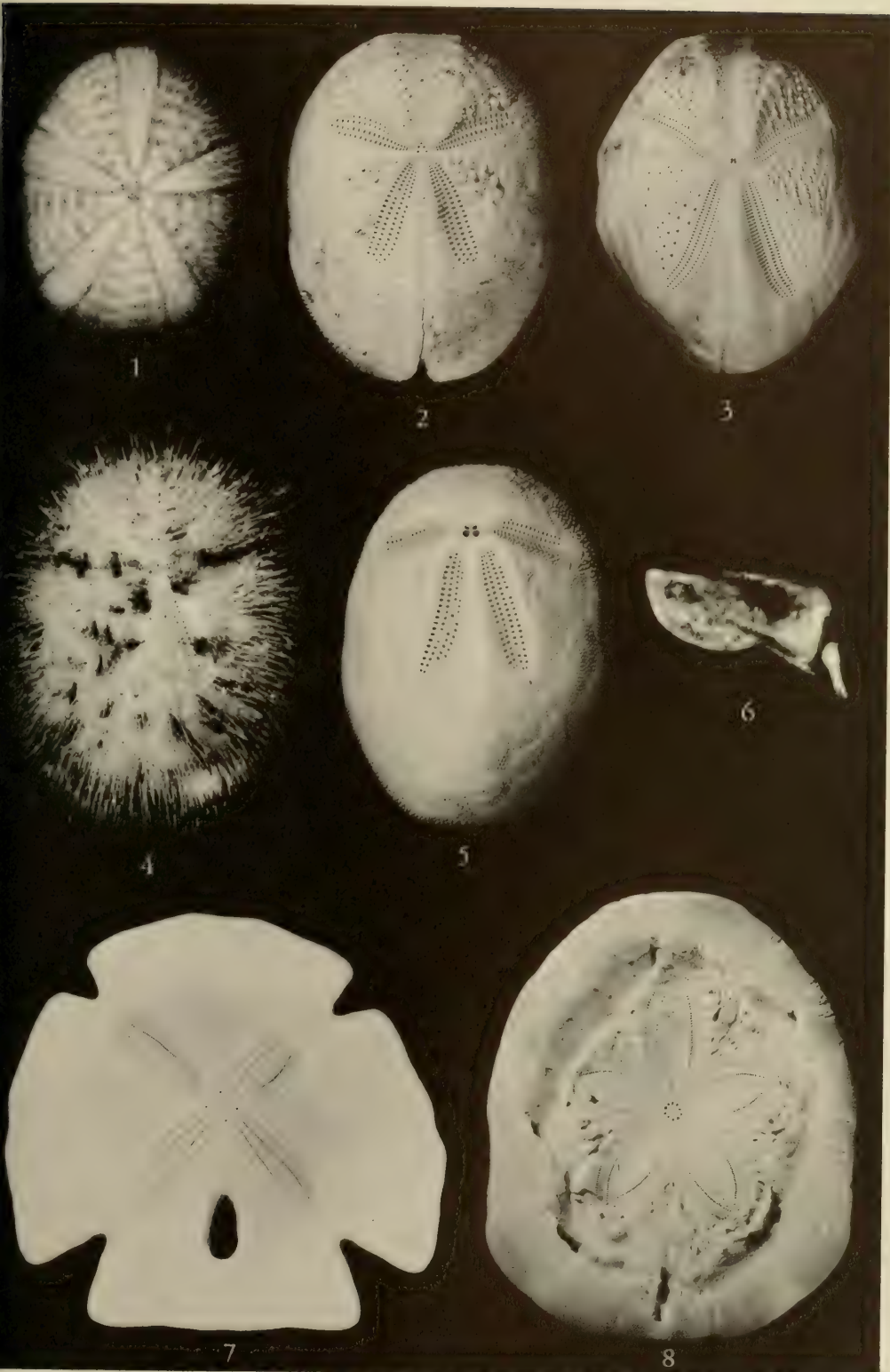


PLATE 15. Six Species of Florida Echinoids  
(See explanation of plate at end of text.)



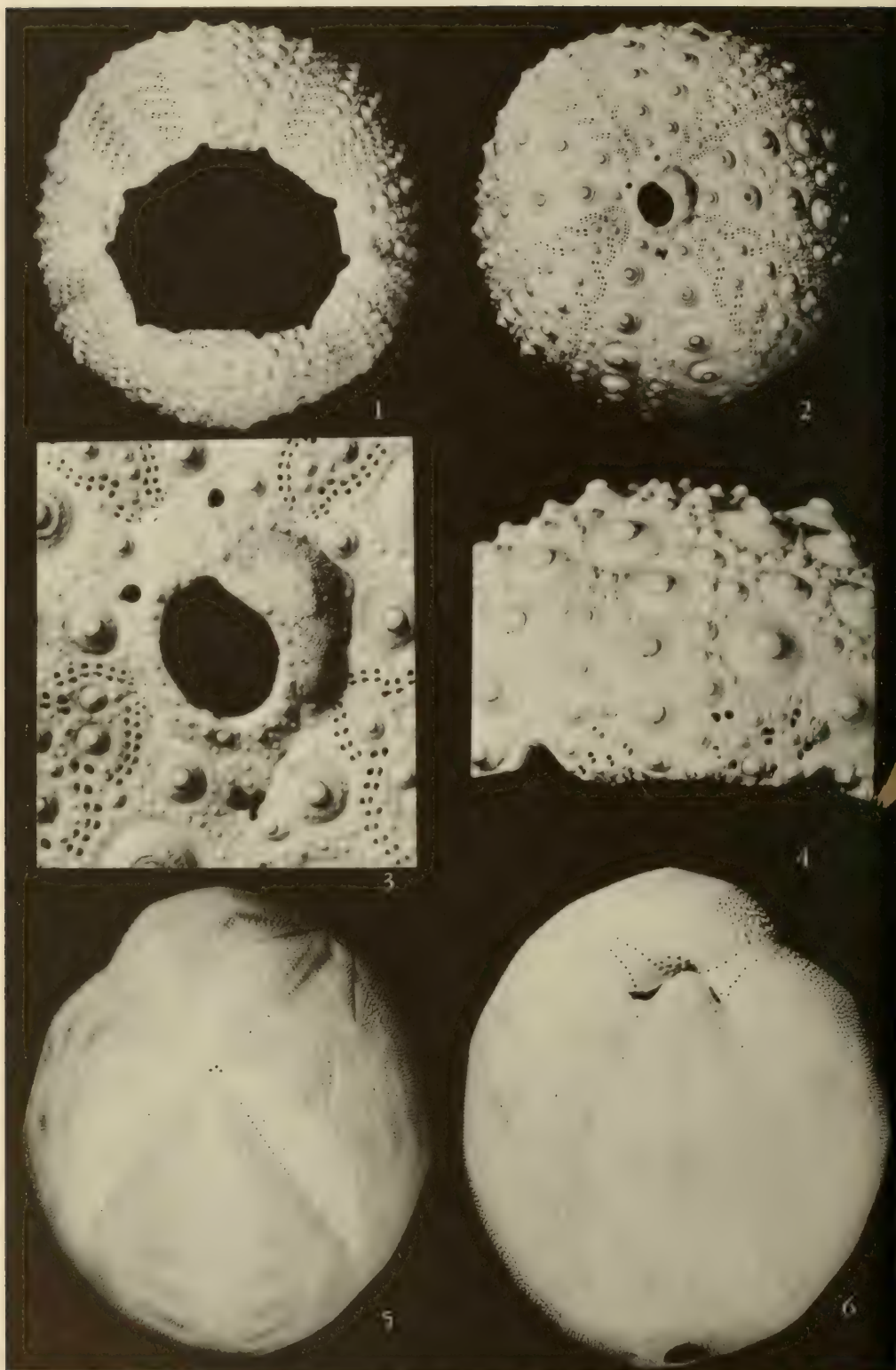


PLATE 16. Abnormal Echinoids—Tetramerous Variants  
(See explanation of plate at end of text.)





SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 149, NUMBER 7

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Charles D. and Mary Vaux Walcott  
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FROM EAST-CENTRAL ALASKA

(WITH 3 PLATES)

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## CONTENTS

	Page
Abstract .....	1
Introduction .....	1
Correlation .....	3
Taxonomic Descriptions .....	5
Literature Cited .....	19
Explanation of Plates .....	21





Charles D. and Mary Vaux Walcott Research Fund

## SILICIFIED ORDOVICIAN BRACHIOPODS FROM EAST-CENTRAL ALASKA<sup>1</sup>

By

REUBEN JAMES ROSS, JR. and J. THOMAS DUTRO, JR.

*U.S. Geological Survey, Denver, Colo., Washington, D. C.*

### ABSTRACT

Silicified brachiopods from the Tatonduk River area, central eastern Alaska along the Canadian border, are possibly of late Middle or early Late Ordovician age. The assemblage closely resembles one described by Schuchert and Cooper (1930) and Cooper and Kindle (1936) from Percé, Quebec, Canada. Many elements are also present in the classical Caradoc section of Girvan, Scotland.

Species of *Dicoelosia*, *Ptychopleurella*, *Cyclospira*, *Ptychoglyptus*, *Diambonia*, and *Christiania* are very like those from Quebec. Except for *Dicoelosia*, which has not been reported previously below the Ashgill in Europe, all the above genera plus *Catazyga* and the species *Anoptambonites* cf. *A. grayae* and *Xenambonites* cf. *X. revelatus* suggest correlation with rocks of Caradoc age at Girvan.

The collection is from a thin-bedded shelly limestone unit in the sequence of Paleozoic strata on the north end of Jones Ridge, Charley River (A-1) quadrangle. The locality has special significance because essentially correlative Ordovician strata exposed along the Tatonduk River 7 miles to the southwest are black graptolitic shales.

### INTRODUCTION

A small collection of silicified Ordovician brachiopods from central eastern Alaska calls attention to a promising area of paleontologic investigation along the Alaskan-Canadian boundary. Although too small in number of specimens to be the basis for definitive conclusions,

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<sup>1</sup> Publication authorized by the Director, U.S. Geological Survey.

the collection has paleogeographic significance and raises important questions concerning intercontinental correlations.

During the summer of 1962, R. J. Ross, Jr., and L. R. Mayo collected Cambrian, Ordovician, and Devonian fossils from the north end of Jones Ridge along the valley of Hard Luck Creek, Alaska. This work was done in support of a mapping program conducted by Earl E. Brabb of the U.S. Geological Survey in the Charley River quadrangle. The general area is north of the Tatonduk River, a tributary of the Yukon, in sec. 9, 15, 16, T. 3 N., R. 33 E., Charley River (A-1) quadrangle (fig. 1). This area was originally mapped

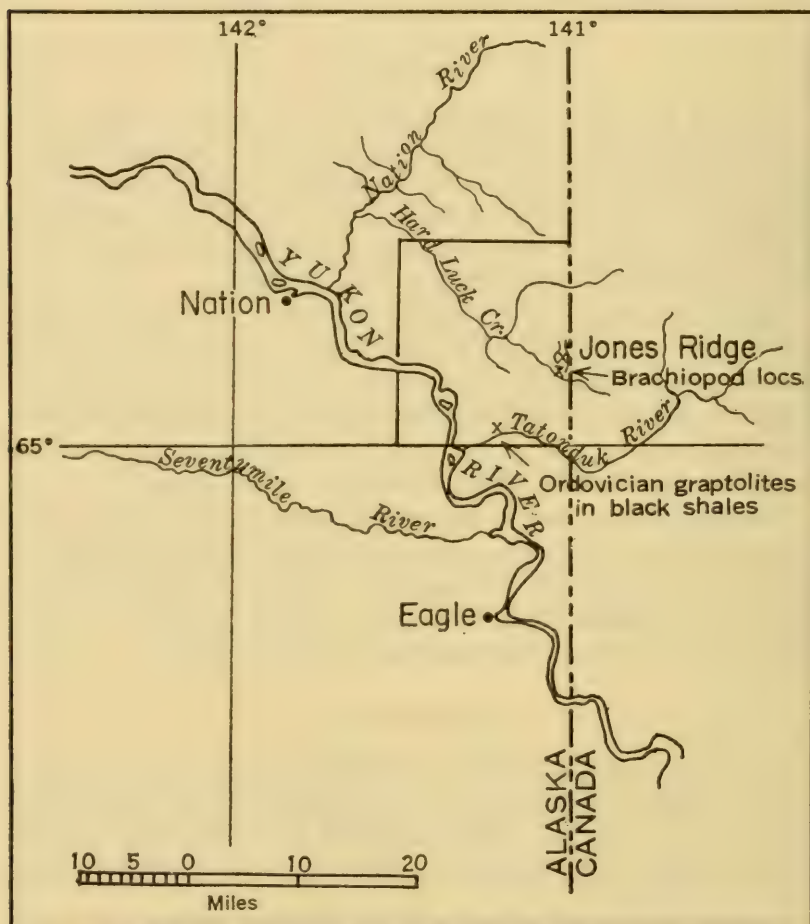


FIG. 1.—Index map, showing relative positions of brachiopod-bearing carbonate rocks and graptolite-rich shales of Ordovician age. Charley River (A-1) quadrangle outlined.

by J. B. Mertie, Jr. (1932, pp. 401-415), who collected fossils from about the same places.

The brachiopods here described are included in USGS collection D1072-CO: altitude approximately 2,000 feet, located 2,000 feet east and 2,000 feet north of SW cor., sec. 9, T. 3 N., R. 33 E., Charley River (A-1) quadrangle, Alaska; from a thin cherty bed approximately 250 feet above the base of Ordovician limestone, south end of Jones Ridge.

Paleozoic strata in Jones Ridge are nearly vertical, dipping south-eastward. Thin- to thick-bedded limestones along Hard Luck Creek range in age from Cambrian on the northwest to Devonian on the southeast. Overlying the limestones are highly contorted Devonian black argillites and cherts which form much of the valley between Jones Ridge on the north and Squaw Mountain 3 miles to the south. Structural complications in this broad area remain to be worked out as a part of Brabb's mapping program.

The Jones Ridge locality is significant because essentially correlative Ordovician strata along the Tatonduk River, 7 miles to the southwest (sec. 10, T. 2 N., R. 32 E.), are black graptolitic shales, an entirely different facies. The Tatonduk River region seems to straddle the boundary between miogeosynclinal and eugeosynclinal deposition during the early Paleozoic (Ross, 1961, p. 335).

This collection of Ordovician silicified brachiopods and corals closely resembles an assemblage from Percé at the eastern end of the Gaspé Peninsula in eastern Canada (Schuchert and Cooper, 1930; Cooper and Kindle, 1936). The assemblage also includes genera and species found previously in the Caradoc of the Girvan District of Scotland (Williams, 1962). Strangely, the nearby Ordovician rocks of Anticosti Island in the Gulf of St. Lawrence, supposedly of the same age, have little in common with those from Percé.

The fossil assemblage is limited because of logistic problems involved in getting large samples out of the area by helicopter. Several species are represented only by immature specimens and others by single specimens. At least 9 species cannot be identified because of inadequate material and 6 of these cannot be assigned to genera with certainty.

#### CORRELATION

Correlation of this small assemblage is difficult and must be considered preliminary. It shares a problem common to the Ordovician in many parts of western North America. The assemblage includes, from a limited stratigraphic interval, genera and species which are



commonly considered guides to either the Late Ordovician or the Middle Ordovician, but not both, as well as other species known to be common to both. Dating such a mixture of species becomes a highly subjective matter because different criteria are invoked by different paleontologists in interpreting the mixture.

The association of *Ptychopleurella*, *Dicoelosia*, *Diambonia*, *Ptychoglyptus*, *Christiania*, and *Cyclospira* suggests close equivalence with the fauna from Percé, Quebec, summarized and dated by Charles Schuchert and described by G. A. Cooper (Schuchert and Cooper, 1930). Revisions and additions to the descriptions were made later by Cooper and Kindle (1936). A review of the original paper by Schuchert and Cooper shows that the Late Ordovician age was based primarily on the occurrence of *Dicoelosia*.

With the exception of that genus, all the other Percé forms, plus *Xenambonites* and *Anoptambonites*, are reported from the Caradoc of Girvan, Scotland, by Williams (1962). It is Williams' conclusion (pp. 57-62) that the Girvan Caradoc can be closely correlated with the Middle Ordovician of eastern North America, equal to the Porterfield, Wilderness, and Trenton Stages of Cooper (1956).

Within the Alaskan assemblage, the following correlations are suggested by genus or species:

Richmond or younger	— <i>Dicoelosia</i>
Cincinnatian or Trenton	— <i>Catazyga</i>
	Leptaenid (Undet. genus B)
Trenton or upper Wilderness	— <i>Anoptambonites</i> cf. <i>A. grayae</i>
Wilderness or Porterfield	— <i>Ptychopleurella</i> cf. <i>P. lapworthi</i>
	<i>Diambonia</i> cf. <i>D. anatoli</i>
	<i>Xenambonites</i> cf. <i>X. revelatus</i>

*Cyclospira* and *Christiania* are typical Middle Ordovician genera, which range, however, into the Late Ordovician. The Late Ordovician occurrence of *Ptychoglyptus* may be questioned, but it is well known in Middle Ordovician strata. Although the age of this fauna is open to review, it is clearly either late Middle or Late Ordovician.

The total aspect of the assemblage is undeniably Caradocian. Perhaps future collections will provide evidence either to extend the ranges of additional Middle Ordovician forms into the Upper Ordovician or to document the occurrence of *Dicoelosia* in older beds. *Dicoelosia* may join *Austinella* and *Catazyga* as genera now known to have their beginnings in the Middle Ordovician.

The only coral in the collection was identified by W. A. Oliver, Jr.

(oral communication, 1963) as an immature *Grewingkia*. In the opinion of Ross it indicates a late Middle or Late Ordovician age.

## TAXONOMIC DESCRIPTIONS

Superfamily ORTHACEA Walcott and Schuchert, 1908

Genus **PTYCHOPLEURELLA** Schuchert and Cooper, 1931

*Ptychopleurella* cf. *P. lapworthi* (Davidson)

Plate 1, figures 2, 4, 6, 8

*Orthis lapworthi* Davidson. Davidson, 1883, Monograph British fossil Brachiopoda, vol. 5, pt. 2, Silurian Supplement, p. 176, pl. 13, figs. 9, 10, Paleontographical Society (London).

*Glyptorthis sublamellosa* Cooper. Schuchert and Cooper, 1930, Am. Jour. Sci., ser. 5, vol. 20, pp. 265-268, pl. 1, figs. 21-22.

*Description*.—Shell biconvex, subrectangular, slightly wider than long; greatest width just anterior of hinge line; anterior commissure gently sulcate; costate with about 12-14 costae on each valve, strong concentric growth lines provide lamellose appearance. Pedicle valve evenly convex with low median fold bearing one strong costa, two lateral costae are intercalated about one-third distance from pedicle beak to anterior margin; lateral slopes with 4-6 costae; low apsacinal area has small open delthyrium; dental plates reduced. Brachial valve with rather shallow median sulcus bearing two costae; cardinalia typical for genus with rather short, slightly curved brachioophores and thin cardinal process.

*Discussion*.—The Alaskan specimens agree closely with those illustrated by Davidson. They are also to a considerable degree like *Ptychopleurella sublamellosa* (Cooper) from the Gaspé. The latter species is slightly smaller and may have a deeper sulcus in the brachial valve. However, size of costae and spacing of lamellae is highly variable within our small sample and we consider *P. sublamellosa* a possible synonym of *P. lapworthi*. Although it is difficult to establish the range of variation within this group of shells because of the small number of specimens—there are only eight specimens in the Alaskan collection—there is enough variation to include not only the Gaspé form but also *P. uniplicata* (Cooper) from the Porterfield. All these specimens could represent a single species. More detailed studies of variation, especially of the Virginia specimens, are needed before this can be demonstrated.

*Figured specimens*.—USNM 145324, 145325, 145326.

Superfamily DALMANELLACEA Schuchert and LeVene, 1929

Genus DICOELOSIA King, 1850

*Dicoelosia jonesridgensis* Ross and Dutro n. sp.

Plate 3, figures 1-5

*Description*.—Shell concavo-convex, deeply emarginate giving exterior the general shape of a maple seed (double samara); length approximately equal to width which is greatest near antero-lateral tips of the extended wings; hingeline short, about half width of shell; area triangular and apsaclinal; valves weakly costellate, about 3 costellae in 0.5 mm, with a single rib more prominent on each wing; commissure crenulated along sides of shell as well as in anterior emargination. Pedicle valve strongly convex, sulcate, crudely pentagonal in outline; delthyrium open, apparently unmodified. Brachial valve deeply concave; anterior crenulation separated from visceral cavity by flanges; cardinal process arises from floor of simple notothyrial cavity and has small expanded knob-like myophore; brachio-phores are slender rods lying along edges of visceral cavity and are seemingly attached to shell for most of length with only the tips free.

*Discussion*.—This species is represented by eight silicified specimens, one of which shows the cardinalia quite well. *Dicoelosia indentus* (Cooper) from the Gaspé is the only other known Ordovician species in North America. The ornamentation of *D. indentus* is coarser than that of the Alaskan form. *D. alticavatus* (Whittard and Barker) as an emarginate anterior like the Alaskan species, but the indentation is far narrower. In addition, the sides of the Silurian shell are more nearly parallel and it is not as strongly concavo-convex in lateral profile. *D. jonesridgensis* is more deeply emarginate than either the Silurian species *D. biloba* (Linné) and *D. oklahomensis* Amsden or the Devonian *D. varica* (Conrad). Illustrations in Hall and Clark (1892, pl. 10, fig. 18) show the brachio-phores as flat blades in the last species, dissimilar to those of *D. jonesridgensis*. However, the cardinalia seem almost identical to those of *D. oklahomensis* as illustrated by Amsden (1951, pl. 15, fig. 6). Brachio-phores of *Dicoelosia lata* Wright from the Portrane limestone of Ireland (Wright, 1964, p. 226, pl. 9, figs. 9, 17) are wider and shorter than those in the Alaskan species; anterior emargination of the Irish species is less pronounced.

*Holotype*.—USNM 145347.

*Figured paratype*.—USNM 145348.



Superfamily SYNTROPHIACEA Schuchert and Cooper, 1931

**Genus CAMERELLA Billings, 1859**

*Camerella?* sp.

Plate 1, figures 11-14, 16

*Description.*—Unequally biconvex with pedicle valve rostrate and brachial valve less convex; outline suboval with beak angle about  $80^\circ$ ; surface nearly smooth with about 6 broad costae developed in anterior half of shell; faint, shallow median sulcus in brachial valve. Pedicle interior with small spondylium; because of silicified secondary material, presence or absence of supporting septum not ascertainable. No brachial interiors obtained.

*Discussion.*—The two specimens in our collection have had much of the original surface of the shells removed in some unknown manner. The anterior commissure is distinctly toothed, indicating 6 costae on the brachial valve, all in the median half of the shell. The faint sulcus in the brachial valve is a feature suggesting pentamerid rather than camerellid relationships. Until more and better preserved specimens can be obtained, the correct taxonomic position of this species must be considered indefinite.

*Figured specimens.*—USNM 145332, 145333.

Superfamily RHYNCHONELLACEA Schuchert, 1896

**Genus RHYNCHOTREMA Hall, 1860**

*Rhynchotrema?* sp.

Plate 1, figures 1, 3, 5

*Description.*—Rhynchonelliform, strongly biconvex, subpentagonal in outline; anterior commissure uniplicate; brachial valve with 10 strong angular costae, 4 low costae of equal height on fold and three on each flank; pedicle sulcus with 3 costae; imbricate ornamentation suggested, although most of exterior has been removed during silicification process. Pedicle interior with strong dental plates, indicated by molds in interior filling. Brachial interior with strong median septum, divided hinge plate; no cardinal process seen, although absence may be due to poor preservation.

*Discussion.*—Unfortunately, the presence or absence of a cardinal process cannot be demonstrated. Although its apparent absence would suggest assigning this shell to *Rostricellula*, the ornamentation and lack of supporting plates argue more strongly for tentative assignment



to *Rhynchotrema*. More material than the single specimen available is needed, especially well-preserved brachial interiors, before proper identification can be made.

*Figured specimen*.—USNM 145323.

Superfamily SPIRIFERACEA Waagen, 1883

Genus **CYCLOSPIRA** Hall and Clarke, 1893

*Cyclospira* cf. *C. glansfagea* Cooper and Kindle

Plate 2, figures 2, 4, 6

*Cyclospira glansfagea* Cooper and Kindle. Cooper and Kindle, 1936, Jour. Paleontology, vol. 10, No. 5, p. 359, pl. 52, figs. 1, 4, 7.

*Description*.—Shell biconvex, subpentagonal in outline; brachial valve with single median costa constituting low fold; narrow sulcus bounded by two low costae on pedicle valve; no other ornamentation. Portion of spire shown in one broken specimen with spire extending well over halfway to anterior margin.

*Discussion*.—All of the specimens at hand are very small as compared with both *C. bisulcata* (Emmons) and *C. glansfagea*. In shape of profile and depth of sulcus they compare favorably with the latter and may represent immature specimens of that species. Larger collections than the present very limited ones will be necessary to indicate their true nature.

*Figured specimens*.—USNM 145337, 145338.

*Cyclospira?* sp.

Plate 2, figures 8, 11, 13

*Discussion*.—A small, smooth biconvex specimen is perhaps assignable to this genus. It has the shape characteristics of an immature individual. Although it is about the same size as the specimens referred to *C. cf. C. glansfagea*, it does not show the characteristic pentagonal shape or sulcus in the pedicle valve. If more material were available, this might prove to be a distinct species of *Cyclospira*.

*Figured specimen*.—USNM 145339.

Genus **CATAZYGA** Hall and Clarke, 1893

*Catazyga homeospiroides* Ross and Dutro n. sp.

Plate 1, figures 7, 9, 10, 15, 17-20

*Description*.—Shell equally biconvex, longer than wide, subovate in outline; costellate ornamentation, with 6 costellae in space of 5 mm

at anterior margin of specimen that is 13 mm long; shell impunctate. Pedicle valve apparently with open delthyrium; remnants of small deltidial plates in a few specimens; small hinge teeth unsupported by dental plates; umbo extended, not incurved. Brachial valve with faint sulcus; interior with divided hinge plate; no evidence of cardinal process; strong median septum extends three-quarters the length of valve; spire with descending lamella in plane of commissure.

*Measurements in mm:*

	Length	Width	Thickness
USNM 145331	12	11	4
USNM 145329	9	10	3+ (broken)
USNM 145327 (holotype)	13	12	8.5
USNM 145330	10	9	—
USNM 145328	6	3.5	2

*Discussion.*—This species is similar to *C. cartieri* Cooper and Kindle in the spacing of radial ornamentation but has only about half as many costellae. The outline of *C. cartieri* is more nearly circular and its pedicle umbo is smaller. *C. homeospiroides* possesses a faint sulcus on the brachial valve, not on the pedicle valve as in *C. cartieri*.

This species is similar to *C. arcana* Williams from Girvan in size and general shape. However, the brachial valve is not as broadly or deeply sulcate and costellation is a little coarser; in *C. arcana* there are about 8 costellae in 5 mm at a distance of 13 mm from the pedicle umbo. In addition, the pedicle valve of the Scottish species is more convex than the brachial, whereas the Alaskan shells are equally biconvex. *Catazyga headi* is more finely ribbed and more rotund, with a widely V-shaped brachial sulcus.

Williams (1962, p. 247) states that adult shells tend to be longer relative to width than juveniles in *C. arcana*, but the opposite seems to be true in the present form, as shown in plate 1, figure 15.

Although the ribbing is coarser than is customary in *Catazyga*, and the brachial valve lacks a pronounced sulcus, this species is placed in that genus. Future investigation may show that several impunctate species now classified within *Homeospira* should be grouped with *Catazyga homeospiroides* as a distinct genus.

Approximately ten silicified specimens and two calcareous specimens of *C. homeospiroides* are the basis for the above description.

*Holotype.*—USNM 145327.

*Figured paratypes.*—USNM 145328, 145329, 145330, 145331.

Genus **WHITFIELDELLA** Hall and Clarke, 1893*Whitfieldella?* sp.

Plate 2, figures 14, 17, 19

Plate 3, figures 6-10, 14, 17, 20

*Discussion.*—A large broken specimen and possibly a dozen clearly immature ones may be referable to *Whitfieldella*. All are characterized by a smooth exterior, oval outline, and biconvex profile. The single large specimen is a broken brachial valve in which there is a very strong median septum originating beneath a divided hinge plate with stout crural bases. There is no cardinal process. What appears to be a subcircular visceral area is actually related to growth of the shell as shown by comparison with the exterior of the valve. More than one species, perhaps more than one genus, is represented by the small specimens. Some are elongate oval while others are almost pentagonal and as wide as long. Some may be young individuals of the species here referred to as *Camerella?*

Additional complete mature valves are needed to determine the correct taxonomic position of these specimens.

*Figured specimens.*—USNM 145343, 145349, 145350, 145351.

Superfamily PLECTAMBONITACEA Cooper and Williams, 1952

Genus **ANOPTAMBONITES** Williams, 1962

In the collections from Hard Luck Creek are several specimens that are obviously closely related to *Leptella?* *grayae*, a species originally illustrated by Davidson (1883, p. 171) partly under two names, *Leptaena grayae* and *Leptaena llandeiloensis*. As pointed out by Reed (1917, pp. 873-874) Davidson included the interior of *L. grayae* (1883, pl. 12, figs. 27a, b) as *L. llandeiloensis*. Jones (1928, p. 489) showed that one of the specimens illustrated by Reed (1917, pl. 13, fig. 14) should be excluded from *L. grayae*.

Jones included *L. grayae* in his genus *Leptelloidea* (1928, pp. 385-389, 399-400) although it differs from all other species in the genus in lack of convexity and "undifferentiated surface ornamentation."

Öpik (1930, pp. 132-133; 1933, pp. 30-32) revised the genus *Leptelloidea* using the characters of the diaphragm in the brachial valve as the most important features. This resulted in a somewhat different grouping of species than that proposed by Jones. Öpik tended to agree with Reed that *L. grayae* probably belonged in *Leptella* Hall and Clarke, although at the time that genus was too imperfectly known for anyone to be sure how it should be classified relative to *Leptelloidea*.



Ulrich and Cooper (1938, pp. 187-191) erected the genus *Leptellina* and presented the first modern description of *Leptella*, with illustrations of *Leptella sordida* (Billings), the type species of *Leptella*. These illustrations show what seem to be two lobes of a bilobed cardinal process in one specimen. Ulrich and Cooper (1938, pl. 39H, figs. 29, 32, p. 188) interpret these to be chilidial plates. They make no comment on the assignments of any European species to *Leptella* other than to question their correctness.

In 1957 Spjeldnaes reclassified many strophomenid genera emphasizing the importance of the pallial markings. Unfortunately, the vascular arrangements of most North American genera and species are undescribed, unillustrated, or unknown. Spjeldnaes's efforts are commendable but have thrown many of our traditional concepts into disarray. His criteria cannot be applied without considerable revision. In this reclassification Spjeldnaes (1957, p. 66) did nothing with *Leptella*, but he placed *Leptellina* in synonymy with *Sampo* Öpik (1957, p. 67-72). However, *Sampo* possesses a denticulate hinge line by original definition (Öpik, 1933, pp. 35-36, pl. 6, fig. 4).

Spjeldnaes (1957, p. 70) also assigned the species *S. indentata* to *Sampo*, noting that it lacked a denticulate hinge and implying that this important feature is of no consequence (1957, pp. 20-22). We do not have the necessary material at hand to effect the revision of American and European forms that Spjeldnaes' work indicates may be needed.

Externally these Alaskan shells cannot be classified with *Leptellina*, *Sampo*, *Leptelloidea*, or *Leptella* because the costellation is of more uniform size and even spacing. They lack the prominent cardinal process of *Leptelloidea* and *Sampo* Öpik (not Spjeldnaes). They possess a rectangular platform in the notothyrium much like that in *Leptella sordida*, with only a faint median groove in the posterior surface of the platform. A chilidium covers the greater part of this platform. The brachiophores are similar to those of *Leptellina*, not to those of *Leptella*. The median septum and circumvisceral flange (brachial lamellae of Öpik) are high, narrow, and nearly perpendicular to the plane of the brachial valve, lacking the ragged lamellose appearance found in the other genera above.

The genus *Anoptambonites* was described by Williams (1962) covering this very interesting group of shells, and the Alaskan specimens fit his descriptions closely. The present occurrence is the first record of the genus in North America.

Roomusoks (1963, pp. 233-235, pl. 1, figs. 1-4) has included in



this genus the species *A. pirguensis*, which lacks the exaggerated elevation of the border of the brachial diaphragm (or lophophore platform) and possesses a somewhat different aspect of the median septum at its confluence with the cardinal process as compared with the type species, *A. grayae* (Davidson). He has also included *Rafinesquina carinata* Høltedahl (1916, p. 25, pl. 2, figs. 4-5), the interior of which has never been described or illustrated. Williams (written communication, Jan. 13, 1964) has accepted the generic assignment of *A. pirguensis*, which we question here, but he joins in questioning that of *R. carinata*.

*Anoptambonites* cf. *A. grayae* (Davidson)

Plate 2, figures 1, 3, 5, 7, 9

*Leptaena grayae* Davidson. Davidson, 1883, Mon. Brit. Fossil Brachiopoda, vol. 5, pt. 2, Silurian Supplement, p. 171, pl. 12, figs. 23-25.

*Leptaena llandeiloensis* Davidson. Davidson, 1883, Mon. Brit. Fossil Brachiopoda, vol. 5, pt. 2, Silurian Supplement, pp. 171-172, pl. 12, fig. 27.

*Leptella grayae* (Davidson). Reed, 1917, Trans. Roy. Soc. Edinburgh, vol. 51, pt. 4, No. 26, p. 873, pl. 13, figs. 10-13, 15-17.

*Leptelloidea grayae* (Davidson). Jones, 1928, Mem. Geol. Survey Great Britain, Paleontology, vol. 1, pt. 5, pp. 489-490.

*Anoptambonites grayae* (Davidson). Williams, A., 1962, Geol. Soc. London Mem. No. 3, p. 171, p. 16, figs. 11, 12, 13, 14, 17.

*Description.*—Valves very gently concavo-convex with finely costellate exteriors; costellae increase by implantation and are of a uniform size; interspaces are narrower than costellae, which number 10 in 5 mm at the front edge of a shell 13 mm long; greatest concavity of the brachial valve is along the midline, producing a sulcate appearance; the posterolateral flanks are flat or very slightly convex; pedicle valve obtusely carinate along the midline and gently convex on the flanks. Pedicle interior with small muscle field as in *Leptellina*; delthyrial cavity with tiny plate close to the apex; pallial trunks originate near the front of each diductor muscle scar, one pair runs forward parallel to the midline of the valve, bifurcating in about 2 mm, the other runs anterolaterally for about the same distance before bifurcation. Brachial interior with strong median septum terminating against the strongly developed, nearly vertical edge of the visceral disk; cardinal process, located on a raised quadrate platform between the brachiorhynchophores, consists of a pair of exceedingly small linear ridges, chilidial plate covers posterior end; brachiorhynchophores slender rods as in typical *Leptellina*; pallial markings strongly incised; two pairs

of prominent vascular trunks originate close to the brachiphores; one pair runs close on either side of the median septum, crosses the circumvisceral ridge, and branches dichotomously twice; the other main pair nearly bisects the visceral area and crosses the boundary ridge before branching. Interior surfaces of both valves covered with fine papillae, probably representing inner ends of pseudopunctae.

*Discussion.*—Additional collections from the area of Hard Luck Creek will undoubtedly produce more specimens of this species. Until we have a larger sample on which to base a new species it seems best to refer these forms tentatively to *Anoptambonites grayae* (Davidson).

*Figured specimens.*—USNM 145334, 145335, 145336.

### Genus DIAMBONIA Cooper and Kindle, 1936

This genus is probably represented in the Alaskan collection by three species. No brachial interiors have been found so that these specimens cannot be distinguished from *Bilobia*. However, associations in the Percé fauna suggest that *Diambonia* is more likely to be present and all three species are assigned tentatively until brachial valves are found.

The three species differ markedly in shell ornamentation. Two specimens possess a single radial costella (*Diambonia* sp. 2); 5 specimens have 5 radial costellae spaced about 1 mm apart (*D.* cf. *D. anatoli*), and one specimen has 3 radial costellae spaced over 2 mm apart (*D.* sp. 1). Although all three may be variants of a single species, the total sample studied is too small to permit a reasonable appraisal of variability until more extensive collecting has been done. Among these specimens a tendency for the smaller ones to possess a larger median septum than the large specimens suggests that septa in the larger specimens may have been resorbed.

Although *Diambonia* is typically a Middle Ordovician genus, *D. discuneata* (Lamont) is reported from Lower Ashgill rocks (Lamont, 1935, p. 316), and *D. septata* (Cooper) is reported from Percé from strata reputedly of Late Ordovician age.

#### *Diambonia* cf. *D. anatoli* Spjeldnaes

Plate 2, figures 10, 12

*Diambonia anatoli* Spjeldnaes. Spjeldnaes, 1957, vol. 37, No. 1, p. 80, pl. 2, figs. 6-8, text fig. 11R.

*Description.*—Pedicel valve strongly convex, wider than long with acute cardinal extremities; ornamented with 5 costellae which, at a

distance of 3 mm from the beak, are approximately 1 mm apart; cardinal angle varies from 55° to 60°; faint and narrow median sulcus barely discernible and occupied by the median costella. Pedicle interior with median septum shaped like a strong rod resting upon a thin blade; there is a suggestion that the supporting blade is subject to resorption. No brachial valves obtained.

*Measurements in mm.*

	Length	Hinge width	Thickness	Cardinal angle
USNM 145340	4	7.5	2.4	± 55°
USNM 145340a	4.2	6.4	2.4	60°
USNM 145340b	4	7	—	—
USNM 145340c	4	7	2.4	+ 55°
USNM 145340d	3	4	1.6	50°

*Discussion.*—This species closely resembles *D. anatoli* Spjeldnaes in size and proportions. Although ornamentation of the Scandinavian species is not illustrated, Spjeldnaes (1957, pp. 80-81, pl. 2, figs. 6-8, text fig. 11R) states that it possesses 5-7 radial costellae. It is not clear whether the number is related to the size of the specimen. If there is no relation it may be impossible to distinguish specimens of *D. anatoli* with 5 costellae from the Alaskan specimens described here. *D. anatoli* is found in Stage 4b alpha of the Norwegian sequence, correlative with the Middle Ordovician Porterfield or Wilderness Stages of North America (Berry, 1960, table 1) and with the lower Caradoc of Great Britain (Dean, 1960, pp. 83-87).

The Alaskan specimens compare closely in size with *Diambonia gibbosa* (Winchell and Schuchert) (Cooper and Kindle, 1936, pl. 51, figs. 9, 10). However, the Minnesota species is more nasute in anterior outline, has strong ridges defining the pedicle muscle area, and possesses 6-7 radial costellae (Winchell and Schuchert, 1895, pp. 416-417, pl. 32, figs. 13-17).

*Diambonia septata* (Cooper) (Schuchert and Cooper, 1930, pl. 1, figs. 9-13) is a relatively longer species, although it also has 5 similarly spaced radial costellae. *D. discuneata* (Lamont) is a larger and wider species than the Alaskan form, with main costellae spaced 0.5 mm apart. A form identified by Williams (1962, p. 173, pl. 16, figs. 25-28) as *D. cf. D. discuneata* from the upper Caradocian has costellae about 1.0 mm apart at a distance of 3 mm from the beak. Its proportions seem closer to those of *D. septata* than to those of Lamont's description of *D. discuneata*.

*Figured specimen.*—USNM 145340.



*Diambonia* sp. 1

Plate 2, figures 15, 16

*Description*.—A single damaged pedicle valve has an outline more transverse than that of other two species, being less than half as long as wide; specimen about 15 mm wide and 6.5 mm long; cardinal angle approximately  $50^\circ$ ; convexity of pedicle valve moderate; surface ornamented with 3 radial costellae which, at a distance of 3 mm from the beak, are spaced about 2 mm apart. Pedicle interior with median septum smaller than in other species.

*Discussion*.—This specimen probably represents a species distinct from the other two described here. The spacing of the radial costellae is wider than in any previously described species. Only *D. discuneata* (Lamont), among described species, has as wide an outline. The convexity of the valve in lateral profile is remarkably low for the genus.

*Figured specimen*.—USNM 145341.

*Diambonia* sp. 2

Plate 2, figures 18, 20

*Description*.—Shell strongly concavo-convex; cardinal angles acute, forming an angle with the hinge line of a little over  $60^\circ$ . Brachial valve bearing a very low, narrow fold, about 0.5 mm wide at anterior margin. Pedicle valve possessing a correspondingly narrow sulcus, in which a single costella is faintly developed; otherwise surface is smooth.

*Measurements in mm:*

	Hinge width	Length pedicle	Length brachial	Cardinal angle
USNM 145342	6.2	3.3	2.8	$60^\circ$
USNM 145342a	5.6	3.8	—	$65^\circ$

*Discussion*.—These are the only known specimens of *Diambonia* with a surface almost completely devoid of ornamentation. Although they may prove to be variants of one of the other species, they are here conservatively separated until larger collections can be secured and studied. One specimen of *D. anatoli* as described by Williams (1962, pl. 16, fig. 24) resembles these Alaskan specimens to a remarkable degree.

*Figured specimen*.—USNM 145342.



**Genus XENAMBONITES Cooper, 1956***Xenambonites* cf. *X. revelatus* Williams

## Plate 2, figures 21-26

*Xenambonites revelatus* Williams. Williams, 1962, Geol. Soc. London Mem. No. 3, p. 191, pl. 18, figs. 21-23, 25.

*Description*.—Shell small, concavo-convex, wider than long, wide-hinged with acute cardinal extremities; anterior margin apparently intraplicate in young stages; valves finely costellate with concentric wrinkles; sharp geniculation near anterior. Pedical valve with fold that has median sulcus in early growth stages; pedicle interior not observed. Brachial valve with shallow sulcus, divided by narrow median fold in posterior part, poorly defined anteriorly; pair of elongate pits occupies sulcus near hinge line; interior with tentlike structure described by Cooper (1956, p. 814), apparently formed by fusing of brachiophores and cardinal process; pallial trunks originate beneath notothyrial structure and run nearly straight forward beneath the margins of sulcus. Largest shell about 9 mm wide (estimated) and 3.7 mm long; geniculation crosses midline at about 3.2 mm.

*Discussion*.—This species is tentatively assigned because only three specimens are available. The complete young shell is supplemented by two broken brachial valves, no separate pedicle valve having been recovered. There is little question of the generic assignment, however.

The Alaskan shells lack the relatively coarse radial costellation of *X. undosus* Cooper, but they possess a much finer radial ornamentation interrupted by irregularly spaced concentric wrinkles. Such wrinkles are not present in *X. revelatus* Williams which has a brachial sulcus divided similarly by a narrow median fold. Two elongate pits are located close to the hinge line in the sulcus in both the Scottish and Alaskan specimens. The manner of anterolateral geniculation is also similar. Where geniculation crosses the midline in *X. revelatus* it produces a narrowly angular pinching of the shell (Williams, 1962, pl. 18, figs. 21, 22). In the largest Alaskan specimen, the geniculation crosses the middle of the shell in a wider curve, but apparently the individual is immature; a more angular form and greater sinuosity probably would be produced by further growth.

*Figured specimens*.—USNM 145344, 145345, 145346.

Genus *PTYCHOGLYPTUS* Willard, 1928*Ptychoglyptus?* cf. *P?* *pauciradiatus* Reed

Plate 3, figures 18, 19

*Ptychoglyptus pauciradiatus* Reed. Reed, F. R. C., 1932, Skrift Norske Vidensk.-Akad. Oslo I. Mat.-Nat. Klasse, No. 4, pp. 122-123, pl. 18, figs. 1, 2.

*Description.*—Shell thin, concavo-convex, roughly semicircular, wider than long with greatest width at hinge line; surface with seven primary costellae between which are many finer capillae; regular concentric wrinkles interrupt the capillae but do not cross the primary costellae; wrinkles are uniform except in the sectors on the ears. No internal structures available for study.

*Discussion.*—A single well-preserved complete specimen is tentatively referred to this species. The Alaskan specimen possesses 7 principal costellae, rather than the 5 of *P. bellarugosus* Cooper from the Gaspé. At a distance of 5 mm from the umbo there are about 20 secondary capillae between the larger costellae. Concentric wrinkles are closely spaced, simple, and aligned transversely from one sector to the next, a characteristic which distinguishes the specimen from many species of the genus as well as from *P. bellarugosus*.

Although one can hardly discuss a species on the basis of a single specimen, it can be noted that this shell resembles *P. virginiensis* in number of primary costellae but that concentric wrinkles are far more regularly and closely spaced. *P. ambiguus* Reed possesses twice as many large radial costellae. In *P. ulrichi* Endo many of the radial costellae are intercalated and closely spaced and concentric wrinkles are very irregular. Costellae are also more closely spaced in *P. shanensis* Reed, in which transverse wrinkles are chevron-shaped within each sector. Larger costellae of *P. valdari* Spjeldnaes are far more numerous than in the Alaskan specimen and the concentric wrinkles are irregularly spaced from one sector to the next.

The specimen from Alaska is very similar to *P. pauciradiatus* Reed both in radial and concentric ornamentation. Reed's species is from the Upper Ordovician Hovin Sandstone of the Trondheim area, Norway. On the other hand, the Alaskan specimen is also similar in ornamentation to an immature (?) shell of comparable size from low in the Caradoc, referred by Williams (1962, p. 160, pl. 14, fig. 34) to *Glyptambonites* aff. *G. glyptus* Cooper.

*Figured specimen.*—USNM 145354.

**Genus undetermined A**

Plate 3, figures 13, 15, 16

*Discussion.*—An interesting small, very wide shell is unique in the collection from Hard Luck Creek. In outline and configuration of anterior commissure it resembles the small shells that can be identified as *Xenambonites* (pl. 2, figs. 21, 23, 25). However, it is much wider at the hingeline and is costellate, unlike the *Xenambonites* species described. Its affinities must remain uncertain until adult shells with this ornamentation are secured.

*Figured specimen.*—USNM 145353.

Superfamily STROPHOMENACEA Schuchert, 1896

**Genus CHRISTIANIA Hall and Clarke, 1892***Christiania* sp.

Plate 3, figure 21

*Discussion.*—A single broken brachial valve assignable to *Christiania* is present in the silicified material from Hard Luck Creek. The exterior is encrusted with siliceous foreign material, but the interior shows two pairs of strong bladelike, divergent plates characteristic of the genus.

*Figured specimen.*—USNM 145355.

**Genus undetermined B**

Plate 3, figures 11, 12

*Discussion.*—A single fragment of a brachial valve exhibits the hinge line, general shape, and brachial apparatus of a leptaenid. Although no other specimens are available, this fragment is illustrated to indicate a potentially important element of the brachiopod assemblage. It is hoped that more specimens will be present in the future collections from eastern Alaska.

*Figured specimen.*—USNM 145352.

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## EXPLANATION OF PLATES

## PLATE 1

(All specimens from USGS coll. D1072 CO)

- Figs. 1, 3, 5. *Rhynchotrema?* sp. Brachial, pedicle, and right lateral views,  $\times 2$ , the only specimen obtained, USNM 145323.
- Figs. 2, 4, 6, 8. *Ptychopleurella* cf. *P. lapworthi* (Davidson)  $\times 5$ . 2, 4. Pedicle and brachial views of a complete specimen, USNM 145324; 6, pedicle interior, USNM 145325; 8, brachial interior, USNM 145326.
- Figs. 7, 9, 10, 15, 17-20. *Catazyga homeospiroides* Ross and Dutro, n. sp. 7, 9, 10. Brachial, pedicle, and left lateral views,  $\times 2$ , holotype, USNM 145327; 15, brachial view,  $\times 4$ , immature specimen, USNM 145328; 17, brachial interior view,  $\times 2$ , showing base of loop, divided hinge plate, and absence of cardinal process, USNM 145329; 18, view through break in pedicle valve,  $\times 2$ , showing part of loop, USNM 145330; 19, 20, exterior and interior views,  $\times 2$ , of a pedicle valve, USNM 145331.
- Figs. 11-14, 16. *Camerella?* sp.  $\times 2$ . 11, 12, 16. Pedicle, brachial, and right lateral views of a complete specimen, USNM 145332; 13, 14, interior and exterior views of pedicle valve, the only specimen which shows the spondylium, USNM 145333.

## PLATE 2

(All specimens from USGS colln. D1072 CO)

- Figs. 1, 3, 5, 7, 9. *Anoptambonites* cf. *A. grayae* (Davidson),  $\times 2$ . 1, 3. Interior and exterior views of a damaged brachial valve, USNM 145334; 5, interior showing only the visceral disc ("lophophore platform" of Williams, 1962) of a broken immature brachial valve, USNM 145335; 7, 9, interior and exterior of a pedicle valve, USNM 145336.
- Figs. 2, 4, 6. *Cyclospira* cf. *C. glansfagea* Cooper and Kindle,  $\times 5$ . 2. Left lateral view of a broken specimen showing part of the spire inside, USNM 145337; 4, 6, brachial and pedicle views of a complete specimen, USNM 145338.
- Figs. 8, 11, 13. *Cyclospira?* sp. Brachial, pedicle, and left lateral views,  $\times 5$ , USNM 145339.
- Figs. 10, 12. *Diambonia* cf. *D. anatoli* Spjeldnaes. Exterior and interior views of a small pedicle valve,  $\times 4$ , showing well developed septum and ornamentation of 5 ribs, USNM 145340.
- Figs. 15, 16. *Diambonia* sp. 1. Exterior and interior views of a pedicle valve,  $\times 2$ , showing relatively short median septum and only 3 ribs, USNM 145341.
- Figs. 18, 20. *Diambonia* sp. 2. Brachial and pedicle views of a complete specimen,  $\times 4$ , lacking any ribs, USNM 145342.
- Figs. 14, 17, 19. *Whitfieldella?* sp. Pedicle, brachial, and left lateral views,  $\times 4$ , USNM 145343.

Figs. 21-26. *Xenambonites* cf. *X. revelatus* Williams. 21, 23, 25. Brachial, pedicle, and anterior views,  $\times 5$ , complete but immature specimen, USNM 145344; 22, fragmentary specimen,  $\times 5$ , showing peculiar distinctive cardinalia, USNM 145345; 24, 26, exterior and interior of brachial valve,  $\times 4$ , USNM 145346.

### PLATE 3

(All specimens from USGS colln. D1072 CO)

- Figs. 1-5. *Dicoelosia jonesridgensis* Ross and Dutro, n. sp. 1, 2, 3, 5. Brachial, left lateral, pedicle, and anterior views of complete specimen,  $\times 5$ , holotype, USNM 145347; 4, brachial interior,  $\times 5$ , paratype, USNM 145348.
- Figs. 6-10, 14, 17, 20. *Whitfieldella*? sp. 6, 8, 10. Brachial, pedicle, and left lateral views,  $\times 5$ , of a specimen possibly referable to *Glassia*, USNM 145349; 7, 9, interior and exterior views,  $\times 2$ , damaged brachial valve, USNM 145350; 14, 17, 20, brachial, pedicle, and left lateral views,  $\times 4$ , USNM 145351.
- Figs. 11, 12. Genus undetermined B. Exterior and interior views,  $\times 2$ , fragmentary brachial valve, USNM 145352.
- Figs. 13, 15, 16. Genus undetermined A. Anterior, brachial, and pedicle views,  $\times 5$ , USNM 145353.
- Figs. 18, 19. *Ptychoglyptus*? cf. *P?*. *pauciradiatus* Reed. Brachial and pedicle views,  $\times 2$ , of the only specimen obtained, USNM 145354.
- Fig. 21. *Christiania* sp. Brachial interior,  $\times 2$ , fragmentary specimen, USNM 145355.



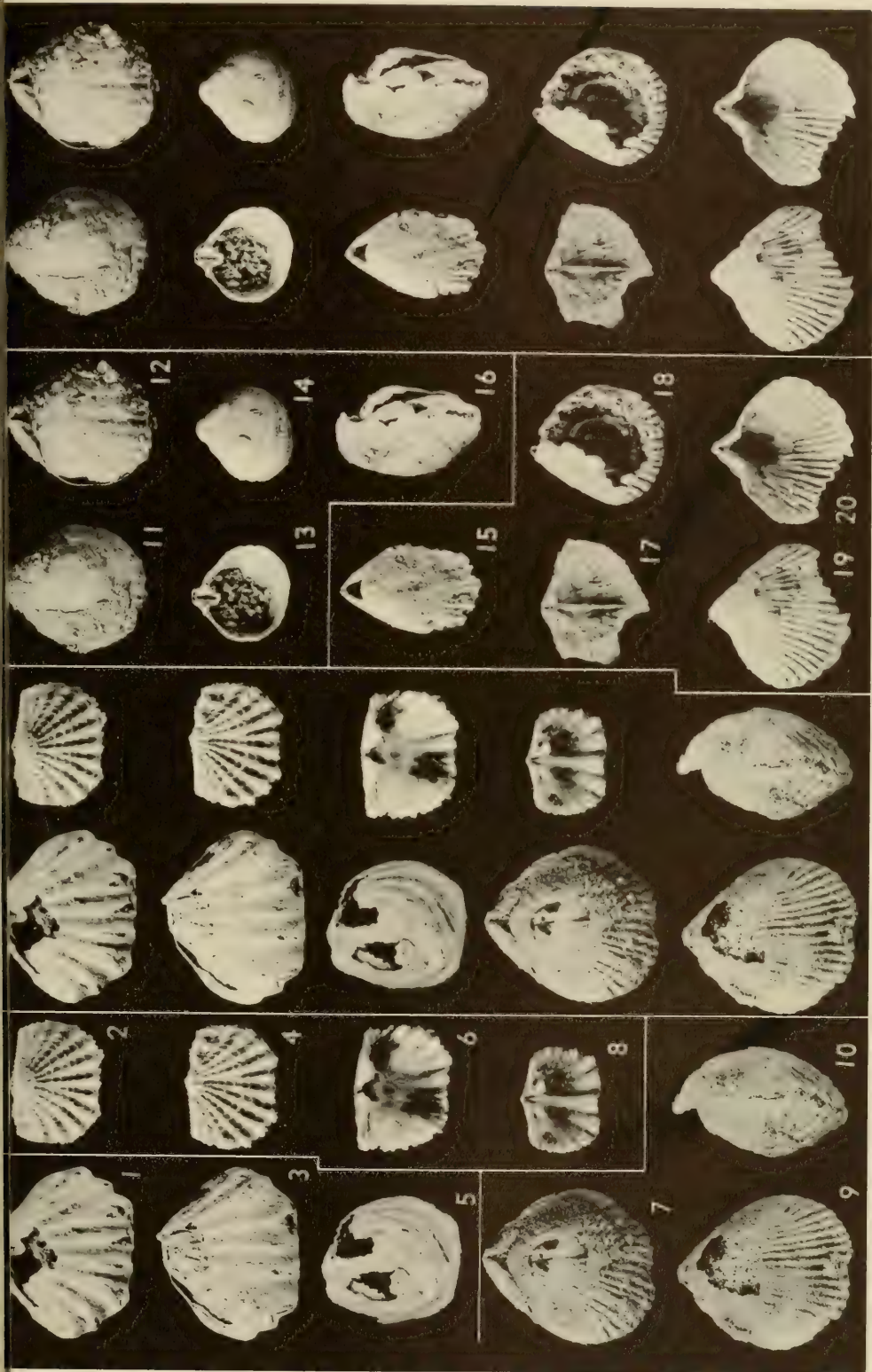


PLATE 1

(See explanation of Plate at end of text.)



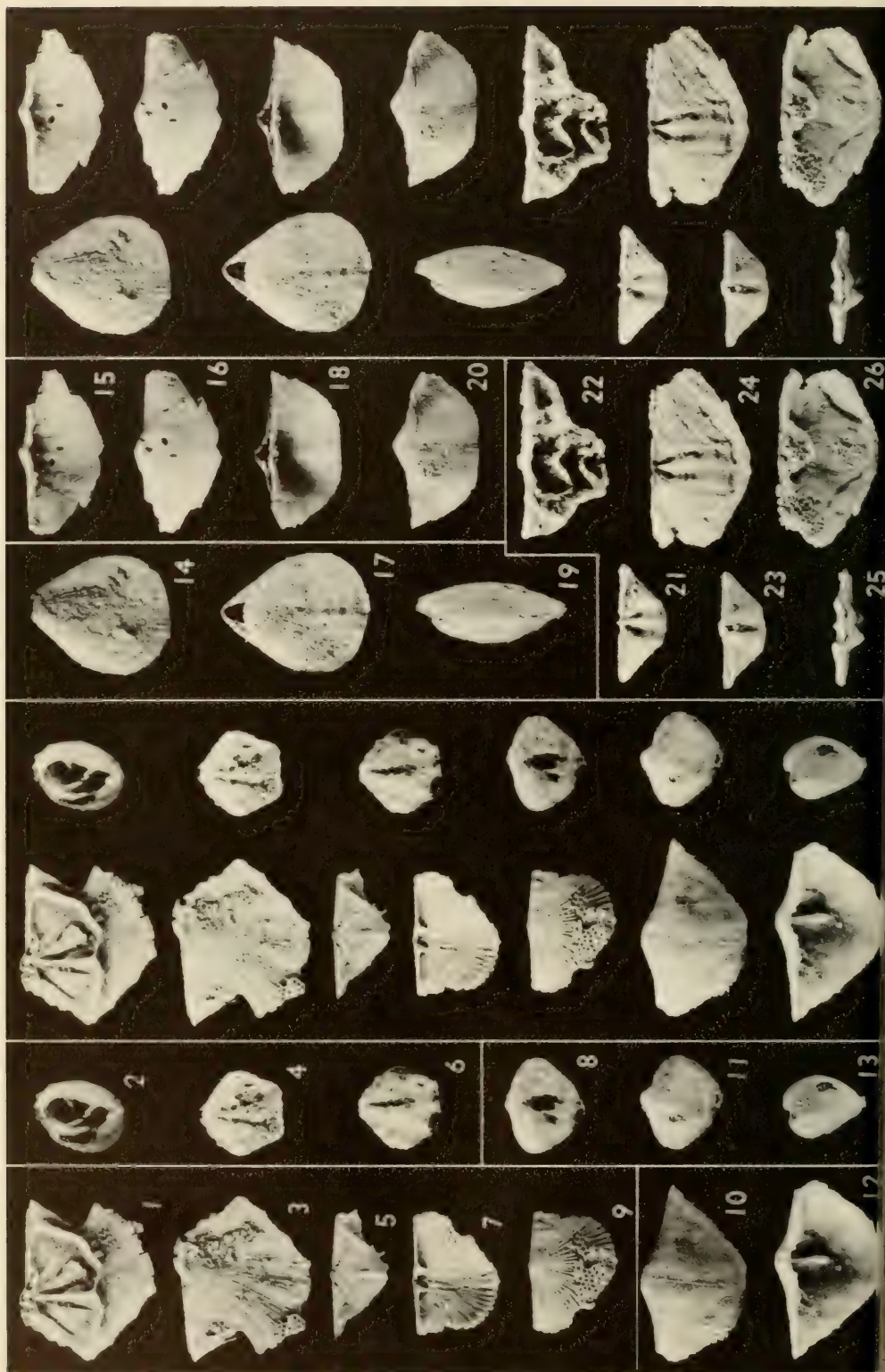


PLATE 2

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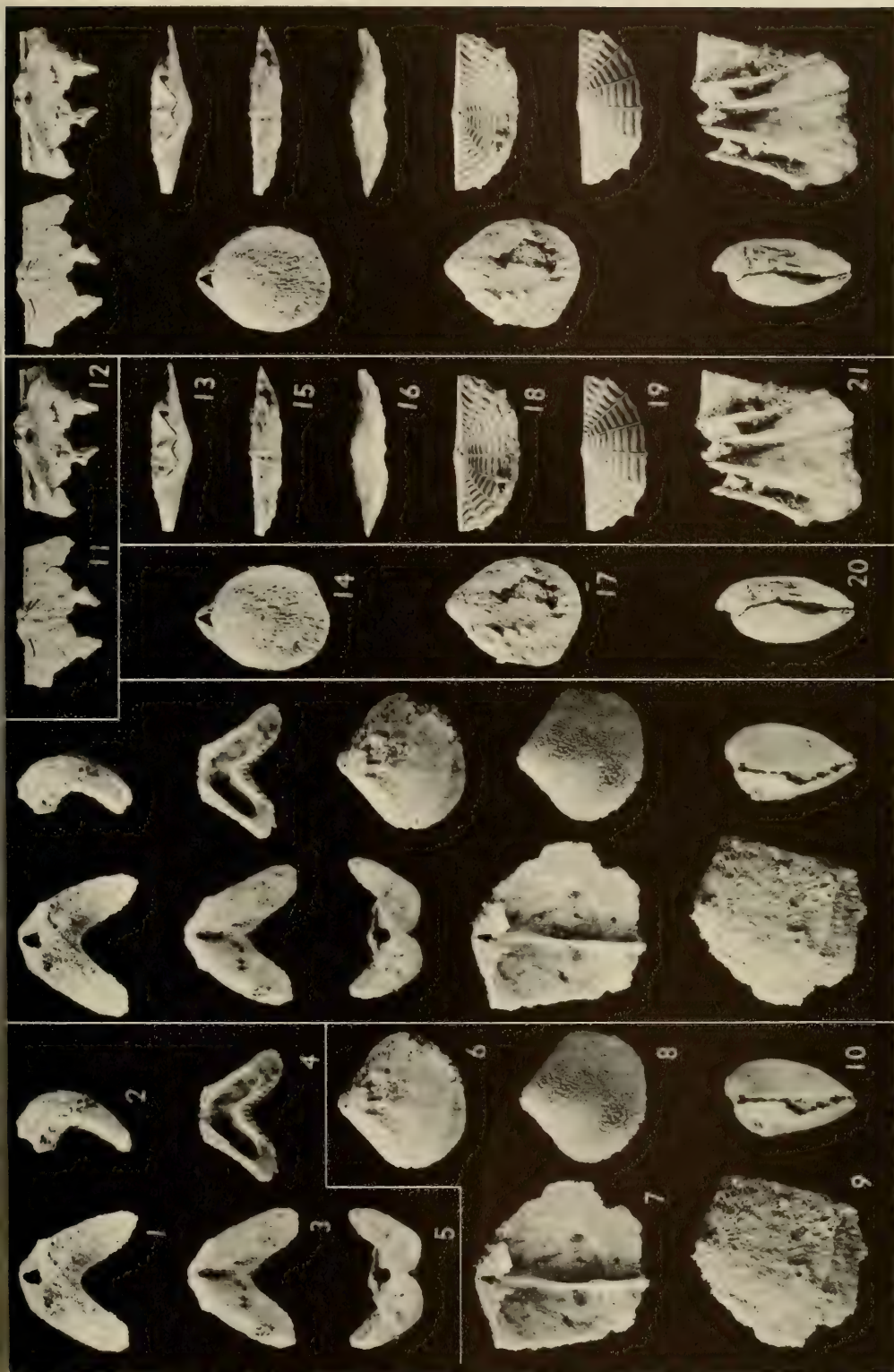


PLATE 3

(See explanation of Plate at end of text.)







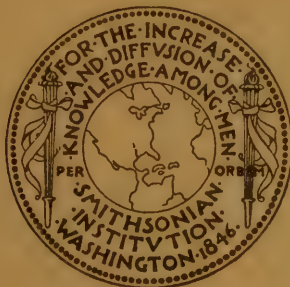


SMITHSONIAN MISCELLANEOUS COLLECTIONS  
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BARTOLOMÉ BERMEJO'S "EPISCOPAL SAINT"  
A STUDY IN MEDIEVAL SPANISH SYMBOLISM

(WITH ELEVEN PLATES)

By  
HERBERT FRIEDMANN  
Director, Los Angeles County Museum



(PUBLICATION 4658)

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# BARTOLOMÉ BERMEJO'S "EPISCOPAL SAINT" A STUDY IN MEDIEVAL SPANISH SYMBOLISM

By  
HERBERT FRIEDMANN  
*Director, Los Angeles County Museum*  
(WITH ELEVEN PLATES)

Since the earliest records of his self-consciousness, man has tended to look upon himself as more than a mere physical being, as a bipartite but yet coordinated union of body and soul. Early in his ascent from savagery to civilization he began to choose natural objects from his surroundings as symbols to convey thoughts or feelings that his language was as yet unable to convey. Much later this long-ingrained habit of "talking in symbols," coupled with the very slow rise of literacy, was accentuated by man's submergence of objective interest in the world about him with the rise of the religiously inspired allegorical and mystical approach that dominated Europe during the long centuries of the Middle Ages. Natural objects, animals, plants, stones, the elements, were not considered interesting in themselves but were looked upon chiefly as the bearers of meanings significant to man, and it was the chief task of scholars to decipher these hidden messages and not to waste time upon their carriers.

It was not until the dawn of the Renaissance that a new interest in the natural world began to assert itself. We must realize that the proliferation and growth of all the natural sciences that we know today would never have come about without this all-important, originally gradual but accelerating mental reorientation from mysticism to objectivity. One of the most fascinating but least explored chapters in the history of science is this transition from the allegorical and the symbolic to the observational and the direct approach to nature. Before this chapter can be written with satisfyingly sympathetic understanding, we need to explore and to elucidate more fully what each specific object really meant to the people who used them, and to trace the alterations in their use and the additional and often unharmonious implications that came to be attached to them. The study of symbolism is a vital part of the history of the emergence of natural science, to the elucidation of which it is hoped the present paper may make a small contribution.

The painting (fig. 1) with which this study deals is a small one ( $18\frac{3}{4} \times 10\frac{1}{4}$  inches), painted on a panel about 1480 by Bartolomé Bermejo. It came to the Art Institute of Chicago a number of years ago as part of the M. A. Ryerson collection. The figure portrayed has not been identified, and none of several suggested solutions is convincing. The saint, richly robed and mitred and with a radiant nimbus, is seated on a narrow, high-backed throne at a desk on which is a manuscript he has been writing. In his upraised right hand is a quill pen; his attitude is that of a writer pausing to think about what to put down next in his text. The decorative inscriptions carried by the figures embroidered on the saint's pluvial identify them as prophets, but this hardly enables us to identify the wearer.

Iñiguez (1935, p. 302) identified the saint as St. Augustine, but Post (1938, p. 874) considered that the habit beneath his cope and the garb of his two companions in the background of the painting were Benedictine. Post, a better art historian than an iconographer, went on to say

the bird behind his desk may be intended as the raven that is one of St. Benedictine's emblems. The Satanic dragon who snarls in the lower right corner would be suitable to Benedict instead of his frequent attribute of the aspergillum by which he discomfited the devil, but it must be remembered that the crushed dragon is the constant symbol of a saint who was appropriated by the Benedictines, Macarius. Sto. Domingo de Salos, also a Benedictine, and the subject of Bermejo's extant picture in the Prado, likewise won many victories over the arch-fiend. The bird certainly looks more like a barnyard fowl than a raven, and may signify still another Benedictine saint—another Domingo—Sto. Domingo de la Calzada, whose ordinary emblems, as tokens of his most stupendous miracle, are a cock and a hen. . . .

However, the bird is neither a raven nor a barnyard fowl but is a very accurate, naturalistic rendition of a European swamp-hen or purple gallinule, the Spanish name for which is *calamón* and the classical name *porphyrio*. The bird has appeared in art very rarely, and then chiefly in faunal and floral compositions by artists such as Roelandt Savery, Jan van Kessel, and Jan Brueghel the Elder, or in decorative tapestries of natural subject matter. Illustrating this here are a detail from an early 17th-century painting by Jan Brueghel the Elder (fig. 2) entitled "Noah's Ark," now in the Walters Art Gallery, Baltimore, and a detail from a French Gobelin tapestry of about 1764 to 1771 (fig. 3) in the Metropolitan Museum of Art, New York (S. H. Kress collection).

In the painting by Bermejo the *porphyrio* (fig. 4) is standing on the floor behind the desk, in the passage between the saint's room and



FIG. 1.—Bartolomé Bermejo. *A Saint*. Art Institute of Chicago.





FIG. 2.—Jan Brueghel the Elder. Detail from *Noah's Ark*. Walters Art Gallery, Baltimore.



FIG. 3.—Detail from a Gobelin tapestry of about 1764-1771. Metropolitan Museum of Art, New York.

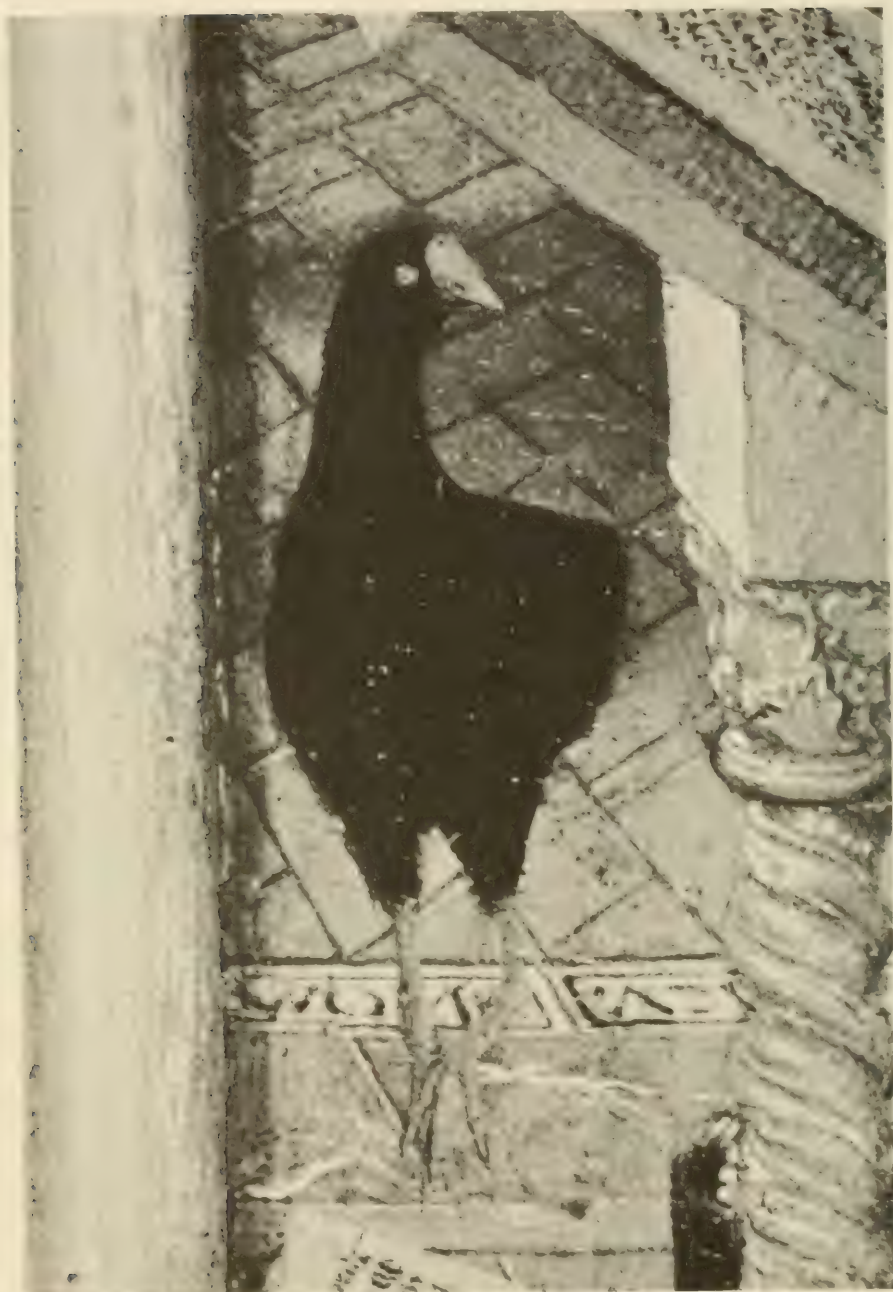


FIG. 4.—Detail from Figure 1.



the outdoors. Its head is turned toward the seated bishop as if watching him. Among the objects on the desk, besides the manuscript on the lectern, are a large book, another sheet of manuscript, a bag of dusting powder for drying the ink, and a compass, while still another book, clamped closed, may be seen through the open door of the base of the desk.

In his study of the legends and descriptions of the birds of the ancient Greek authors, Thompson (1895, p. 152) writes that the porphyrio was considered a bird of lofty morals and great vigilance. He refers to pertinent statements in the works of Aelian (XXXV, 14), who considers the bird to be very chaste and modest, and notes that the bird was said to be held sacred in Lybia. He also cites Dionysus as another describer of the virtues of the porphyrio but does not mention Aristotle. In the latter's writings (*History of Animals*, trans. R. Crésswell, 1902, pp. 45, 206) I find only that this bird has a long neck and, unlike other birds which imbibe water at intervals, raising their heads in order to swallow each mouthful, it gulps down directly and continuously without lifting its bill from the water. The virtues ascribed to the porphyrio by Aelian, Dionysus, and others could easily apply to a great many saintly individuals serving in high church offices. Of more immediate pertinence to its usage in this painting is the identification of the porphyrio with Pudicitia, representing modesty and chastity, in the famous emblem book of Andrew Alciati (fig. 5), a primary source of concepts and symbols for many artists painting after the middle of the 16th century. This book was hardly completely a personal invention of Alciati's and must have included and reflected the thoughts and emblems that had been current for some time before then.

Thus, even though Bermejo's picture was painted some decades prior to the first appearance of Alciati's work, it is important to give serious consideration to the concept of chastity as embodied in the porphyrio in the picture of the episcopal saint. For if, as seems highly probable, the porphyrio does connote chastity, this would cast doubt on the correctness of Iñiguez's assumption that the writing bishop was intended to be St. Augustine, whose difficulties with continence caused him to utter his famous prayer "Lord, give us chastity, but not yet."

One further point about the porphyrio may be made: Its Greek name Porphyryon, its Spanish name Calamón, and its French name Poule Sultan all refer to its purple color. Aside from its other connotations, its coloration makes it peculiarly fitting as a companion bird to a bishop, who traditionally has purple vestments as part of his garb.



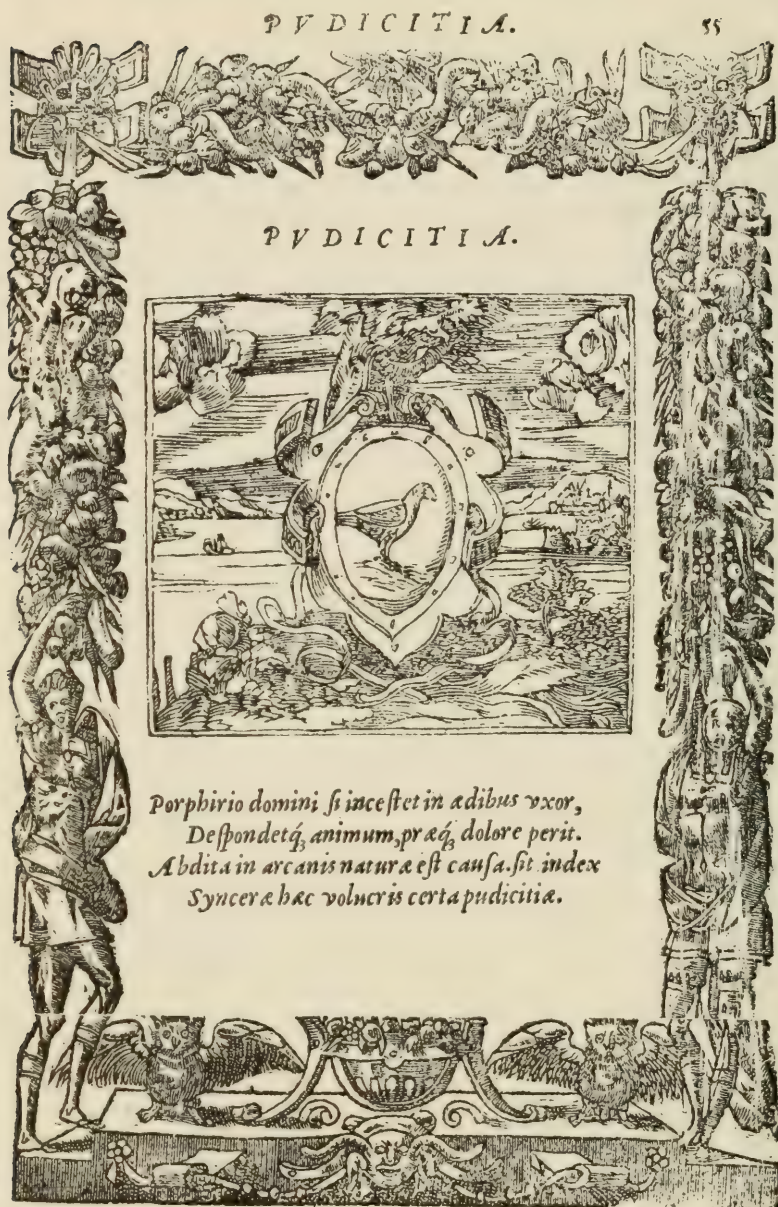


FIG. 5.—Page from the emblem book of Andrew Alciati.

In the upper left portion of the arch framing the door leading from the saint's room to the corridor beyond is a small cage with a bird in it. This is a borrowing from Italian, Flemish, and Germanic iconographic usage and is a motif that appears to occur very rarely in Spanish painting. The concept of the small bird in a cage is a symbol of the human soul imprisoned in the body, awaiting the release that comes with the promise of redemption after death. Bergström (1957) and, earlier, Male (1928) have shown that this concept stems from medieval allegorical representations of Hope (*Spes*), often shown as a woman standing on a cage containing one or more small birds, and sometimes with a ship on her head, a spade in one hand, and a bee-hive in the other, as in our figure 6, taken from a miniature of 1511 in the royal library in The Hague (Ms 76E13), reproduced in Bergström's study of the symbolism of the caged bird. In this illuminating paper Bergström demonstrates that the motif of the caged bird probably entered into the iconography of the Madonna before that of *Spes*. That it became associated with the concept of Hope undoubtedly strengthened its usage in connection with pictures of the Madonna. We can also point out, as collateral argument, that the Madonna was frequently referred to as "*Sancta Maria, nostra spes vera*" (Holy Mary, our true hope). A somewhat later, more mundanely philosophical parallel concept, but not demonstrably derivative, is expressed by Leonardo da Vinci on a sheet of drawings of birds in cages (*Codex Atlanticus*, 68, v., b.) where he writes "the thoughts turn toward hope" (*I pesieri si voltano alla speranza*).

In the present picture the bird in the cage is definitely identifiable as a goldfinch. As shown in an earlier study (Friedmann, 1946, pp. 46-51) this bird was used in Spanish art from the middle of the 14th to the middle of the 17th century. It was the most frequently chosen bird in Italian devotional art because it not only represented the human soul but was a symbol of resurrection as well, and particularly because it came to be used as a sign of protection from the plague. From Italy this use of the goldfinch was carried to Spain by the early Florentine painters, such as "Starnina" and his contemporaries, and by the Sienese artists who worked nearby in southern France, chiefly at Avignon, whence their influence spread westward. Post (1930, pp. 177, 182) was led to conclude that the Italianization of late Gothic painting of the 14th century was more noticeable in Spain than almost anywhere else in Europe. The little goldfinch was one of the pictorial devices these Italian artists introduced into Hispanic art.

The caged goldfinch in the Bermejo picture reminds one of the detailed intarsia panel (see fig. 7) by Fra Giovanni da Verona in the



**E**spérance sur le monde est oïseuse  
 Compaignie a son aussi de charité  
 Et toutes fois d'une vertu esgale  
 Je vous prie ces sommes en verité  
 A voir trespassez lae q'as tu merité  
 Qui ferite  
 Ne tint de gens par tel cas fortune  
 En estant cil qui les a instruits  
 Bien les desfruits  
 Et de toi ont moult cause de ce z'undre  
 Faisant clameure et piteables cries  
 Et leurs habits toie de noir faire tandre

FIG. 6.—Miniature of 1511 in the royal library at The Hague.





FIG. 7.—Fra Giovanni de Verona, intarsia panel in the choir of the church of Santa Maria in Organo, in Verona.



choir of the church of Santa Maria in Organo, in Verona, said by Bergström to date from 1499, somewhat later than our painting. It also recalls the early German portrait of a man with a caged bird, practically synchronous with the Bermejo, in the fine arts museum of Strasbourg. This picture, discussed at some length by Naumann (1934) and by Bergström (1957), has a caged bird, not a goldfinch but apparently a thrush, above and behind the man's head, and has the words "Ora pro me" (pray for me) in conspicuous letters placed near the mouth of the sitter, certainly an indication of hopefulness.

It is significant that a "healing" bird, or a "savior" bird in time of plague, should be the kind used by Bermejo, as there is other evidence that the saint reproduced was a person who, in addition to being a great scholar, was obviously much interested in the natural sciences, as indicated by the compass on his desk, and especially in medicine, as suggested by the activities of his underlings in the background—one monk apparently concocting some kind of herbal medicine over a fire and the other sorting plants brought in from the garden.

The floor of the arched opening at the back of the room leading to the outdoors is raised. There are letters on it forming incomplete words which are quite undecipherable, although one word, interrupted by the stand of the bishop's lectern, might be completed to read "medicus." If this is the case, it complements the ideas suggested by the presence of the healing bird and by the activities of the two monks. The combined implications of a scholarly, literary bishop, interested in natural science, particularly those aspects of it that relate to medicine, all suggest that the man portrayed is Saint Isidore of Seville, the author of one of the earliest and greatest of the medieval encyclopedias, the *Etymologiae*. Some years ago, when I first became interested in this possible identification, Dr. Erwin Panofsky reminded me (*in litt.*) that the medically pertinent sections of the *Etymologiae* were known and separately copied as *liber Isidori episcopi de medicina*, as, for example, in the Durham Ms. Hunter 100.

In identifying the saint as Isidore the following thoughts are worth mentioning. In Medieval and early Renaissance culture a certain degree of interest and significance was attached to some words having more than one meaning. What today would be dismissed as a play on words or a pun was then looked upon by some as meaningful, as a common denominator, as it were, between otherwise divergent concepts. I have already noted that the porphyrio was known both as *calamón* and as *porphyrio*, both names referring to its purplish color. It so happens that in his *Etymologiae*, Isidore makes frequent reference to some of the writings of the noted Latin author Por-

phyrio, especially to the *Isagoge* of this 3d-century writer (ca. 233-304 A.D.). The *Isagoge* had been translated with a commentary by Boetius, and this became one of the favorite textbooks of the early sermonizing scholastics (Sarton, 1927). Porphyrio was originally named Malchos, but his teacher, Longinus, considered him worthy of a nobler name and called him Porphyrio, "the purple clad." It may thus be that the bird porphyrio, watching the writing Isidore, is also a remembrance of one of his sources, the author of the *Isagoge*.

Furthermore, in his *Etymologiae* (libro VI, "de la retorica y dialecta," capitulo xiv) Isidore describes the quill pen by saying "Se llama calamo porque pone la tinta sobre el papel" (it is called calamo because it places the dye [ink] on the paper). Calamo (really a quill), a Spanish word no longer in use, was apparently still a part of conversational vocabulary in Bermejo's time. Thus the common name of the gallinule in Spanish, calamón, may have served to reflect the very act in which the saint is engaged in our painting.

It must be admitted that although Isidore describes and discusses a number of kinds of birds in the *Etymologiae* (libro 12, capitulo 7, "de las aves") he does not mention the gallinule or refer to the names calamón or porphyrio. Nor was the porphyrio used emblematically by such "source authors" as Ripa or Camerarius, although it was by Alciati.

Boetius's translation and commentary on Porphyrio's "*Isagoge*" or "*Introduction to the Categories of Aristotle*" served as a major force in the introduction into the cultural, intellectual life of western medieval Europe of the basic concepts and data of much of Aristotelian philosophy. Taylor (1938, p. 45) refers to the *Isagoge* as a "corner-stone of the early medieval knowledge of logic." That Porphyrio's writings were so thoroughly accepted and absorbed into the compilations of ecclesiastical encyclopedists like Isidore of Seville is all the more noteworthy since Porphyrio was not only a pagan, non-Christian writer of the early centuries of Christianity but was also known as the author of an admittedly rational and penetrating book directed against the Christians and their beliefs. In spite of this probably uncomfortable fact it was recognized that in some of his discussions he reached heights as truly spiritual as those of any "safer" authors secure within the embrace of the Church. His idea of sacrifice is a case in point. In one passage ("De abstinentia," ii, 34) he wrote (translated by Taylor, 1938) that the perfect sacrifice is to disengage the soul from passions. Chastity and asceticism were adhered to rigorously by him. The use of the purple gallinule

as an emblem of chastity certainly adds to its fitness as a sign of Porphyrio, whose name it shares. The same virtue was also a characteristic of St. Isidore, with whom the bird is associated in Bermejo's painting.

At the end of the left arm of the saint's throne is a gigantic snail (fig. 8), unusual iconographically for its great size and in that the animal is shown largely extruded from the shell. The exaggerated size seems due to the artist's intention to use it as a decorative up-curved knob-like ending of the throne arm as well as to place it in the picture for its symbolic content. The fact that the snail itself is shown coming out of the shell and moving up the arm of the chair, away from the direction of the lectern on which the saint's manuscript is lying, suggests that the text of the manuscript is something from which the meaning implied in the snail is trying to escape, or, in more general terms, that the content of the writings and the symbolism of the snail are mutually incompatible.

The snail had two quite different connotations. It was a symbol of sloth, and especially of those souls who, by their sluggishness, appear to attach themselves too greatly to the good things of the world and do not attempt to seek after the higher things of the spirit. This concept may be looked upon as something not in accord with the writings being penned by the saint. The snail was also used in quite an opposite sense, as is so often the case with symbols. It became looked upon as a symbol of Christ, for the following reason. One of the earliest and most influential of the early Church writers, Tertullian (*Apologeticus*, xlviii), took over from the old classical source of the Delphic oracle the judgment that the snail is the emblem of those who die and rise again from the tomb (cited by Charbonneau-Lassay, 1940, pp. 930-931, as taken from Dom. H. Leclercq, *Dictionnaire d'Archaeologie chrétienne*, t. 3:2:col. 2906). The belief that the snail remained for three months in the ground during the winter, and then, when the warmer weather of spring began to make conditions more equable, it came out again, was used as a parallel to the three days of the entombment of Jesus prior to the resurrection. Furthermore, the fact that the snail shell has a lid, or operculum, which it keeps closed while lying in the earth but which it is able to open when it wishes to emerge and move about, was seized upon as akin to the raising of the cover of the tomb at the time when Christ rose from the grave. The shell of the snail thus came to signify the tomb whence man shall arise on the Day of Redemption. The snail emerging from the shell thus would seem to imply the act of Resurrection. That the artist chose to show the



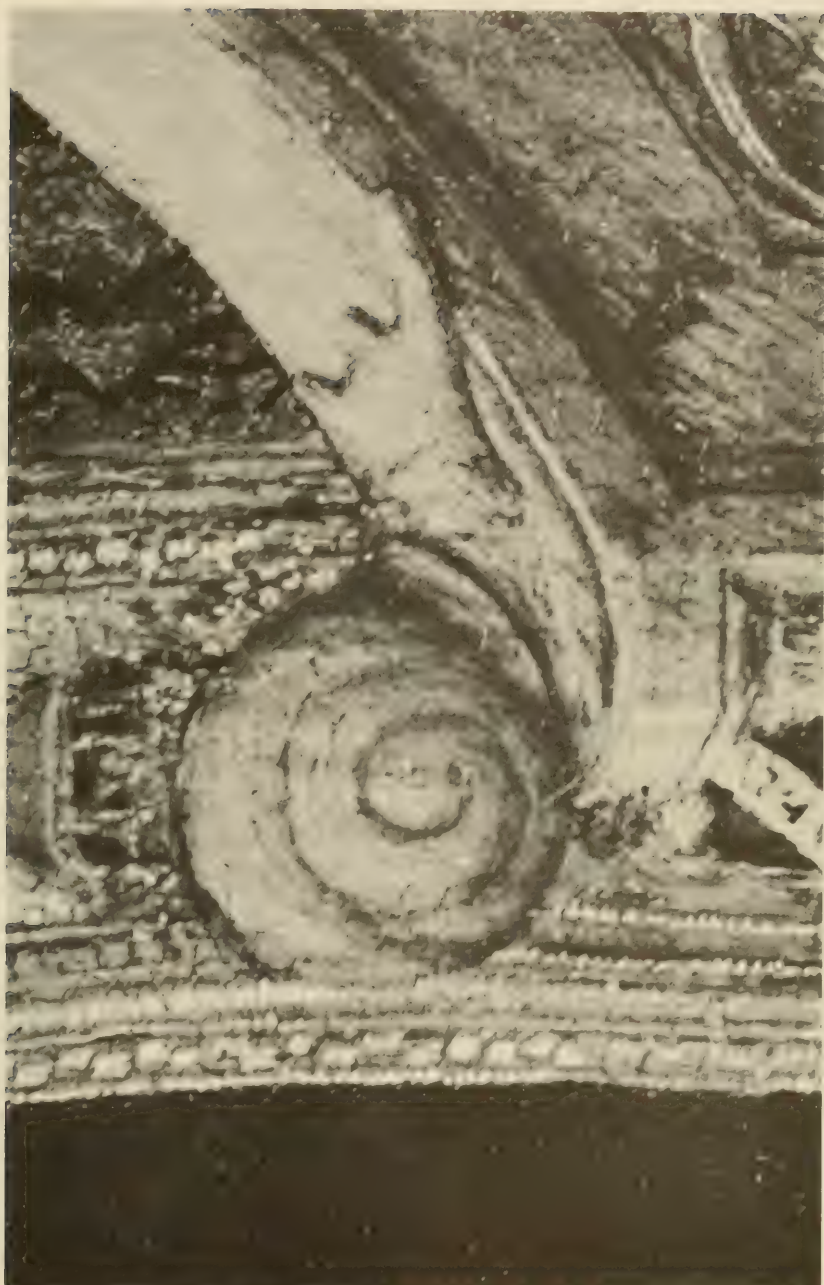


FIG. 8.—Detail from Figure 1.



animal in the act of emerging certainly stresses this idea, as the shell itself would have been sufficient to convey the tomb symbolism and would also have been ample as a naturalistic motif to serve as a part of the decoration of the throne. Furthermore, the artist has given the head of the snail a strikingly tripartite appearance as if to further emphasize the trinitarian number involved in the three months of hibernation and the three days of entombment. For a fuller discussion of the symbolism of the snail, both mundane and spiritual, the interested reader may be referred to Charbonneau-Lassay (1940, esp. pp. 930-931).

It is in this sense of a "resurrection" symbol that the snail appears in an inconspicuous place in the lower right foreground of Perino del Vaga's altarpiece *The Nativity* (figs. 9, 10) in the National Gallery of Art (S. H. Kress collection). The inconspicuousness of it in that picture, where it remains unnoticed by the majority of viewers, is in striking contrast to its enlargement and placement in Bermejo's panel.

A further pictorial connection between the symbolism of the snail and the tomb of Christ exists in Bermejo's painting. The decoration on St. Isidore's pluvial that appears immediately above and behind the snail shell depicts a domed tomb-like structure, an omphalos, supported by pillars. As was clearly pointed out by Smith (1950, p. 76) in his study of the use and symbolism of the dome as an architectural design, ". . . the Christians at Jerusalem came to associate the ideas of an omphalos with the domical tomb of Christ, the ciborium over the altar and the Mount of Calvary. . . ."

The crushed, snarling dragon (fig. 11) is an old and widely used symbol of wrath and evil, and, as such, occurs in religious art with numbers of saints as a sign of one of the vices they overcame by their piety and good deeds. Thus, to take but a single example, St. Servatus is usually shown seated at a desk with a dragon under his foot. Other saints that quickly come to mind in this connection are Margaret, Martha, Philip, and Sylvester, and the archangel Michael. St. George of Cappadocia is usually shown in the act of transfixing the dragon with his lance. The dragon is thus of no special significance, other than in its general connotation, in this painting by Bermejo.

Because of the richness of symbolic creatures portrayed in this picture, the rarity in religious art of one of them, the porphyrio, the unusual use and magnitude of the snail largely extruded from its shell, and the rare use by Spanish artists of the motif of the caged bird (and especially the caged goldfinch), one wonders how and



FIG. 9.—Perino del Vaga. *The Nativity*. National Gallery of Art (Kress Collection), Washington.



FIG. 10.—Detail from Figure 9





FIG. 11.—Detail from Figure 1.



where Bermejo obtained this knowledge with which he endowed his painting of St. Isidore. There is nothing in Tormo y Manzo's study (1926) of the artist, the most extensive one to date, that provides any suggestion. He merely categorizes our painter as the last of the primitives, hardly a characterization to evoke assimilative scholarship as one of the artist's traits. Though some students have assumed that Bermejo may have had some contact with early Flemish painters, or, at least, with some of their work, this is only an assumption.

By and large Spanish use of symbolism was more direct, more explicit, and more emphatic than was generally the case with artists in Flanders, France, or Italy. A case in point is the use of the partridge by Juan Pantoja de la Cruz in his painting of St. Nicholas of Tolentino that I had occasion to discuss in an earlier paper (Friedmann, 1959). This almost tediously matter-of-fact attitude makes one truly wonder what an Iberian artist of the last years of the 15th century would have felt constrained to do when designing a picture of the most scholarly and erudite of all medieval Spanish ecclesiastics. It seems that Bermejo responded to this need by introducing into his panel many allusions to the intellectual conceits of learning, surrounding the great encyclopedist with symbols congenial to his work and character. Whether Bermejo did this alone, or with the assistance of more learned advisors, it is impossible to say. The result is, however, an intellectual credit to the final years of "primitive," pre-Renaissance painting in the Iberian peninsula. The picture was intended, in all probability, for a church school or seminary as the use of some of its symbolic contents are sufficiently unusual as to suggest that they might have been beyond the comprehension of the average lay person.

For assistance in gathering the photographs illustrating this paper, I am indebted to the Art Institute of Chicago (particularly to Mr. Waltraut M. Van der Rohe), the Walters Art Gallery, Baltimore, and the Samuel H. Kress Foundation (especially to Miss Mary M. Davis), New York. I am indebted to Charles P. Parlshurst for calling my attention to the omphalos and to the book by E. B. Smith.

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Charles D. and Mary Vaux Walcott  
Research Fund

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FROM NEBRASKA

By  
LESTER L. SHORT, JR.

Systematic Ornithologist, U. S. Fish and  
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# A NEW PLIOCENE STORK FROM NEBRASKA

By

LESTER L. SHORT, JR.

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Curator, Smithsonian Institution*

During 1956 Dr. Charles G. Sibley, visiting the University of Nebraska campus, borrowed from the Nebraska State Museum a number of avian fossils in that collection, with the intent of studying them. Subsequently Dr. Sibley gave me permission to undertake identification of the fossils, which included specimens from the Oligocene to the Pleistocene of Nebraska. Through the kindness of Dr. C. B. Schultz of the Nebraska State Museum and Dr. Sibley, I have been able to borrow these fossils for continuation of my investigations at the U. S. National Museum. One of them, a distal tibiotarsus, proves to represent a new genus and species of stork, which is herein described and compared with fossil and extant storks.

Family CICONIIDAE

Subfamily Ciconiinae

**DISSOURODES**, new genus

*Diagnosis.*—*Dissourodes* is most similar to the modern genus *Dissoura* Cabanis 1850, but distal tendinal groove opening in direct contact with deepest part of intercondylar fossa, not separated from it by a ridge between that opening and the intercondylar tubercle (as it is in *Dissoura*). Internal condyle distally angles toward the opening of the tendinal groove in *Dissourodes*. *Dissourodes* is much larger than *Dissoura episcopus*. Other characteristics of the genus are those given below for the type species *Dissourodes milleri*.

**DISSOURODES MILLERI**, new species (fig. 1)

*Holotype.*—Distal 162 mm. of left tibiotarsus, Nebraska State Museum No. 5780. The distal 135 mm. of the tibiotarsus is complete except for some surface abrasion, slight wear at various edges, and a missing intercondylar tubercle. The proximal portion of the bone

is broken diagonally for 27 mm. This distal tibiotarsus represents an estimated 40 to 50 percent of the original bone. The fossil was collected on July 18, 1930, by Paul McGrew and Phillip Harper at a quarry four miles southeast of Valentine, Cherry County, Nebraska, SEC. 17, T. 33N, R. 27 W. It comes from Cr-12 in the Valentine formation of the Ogallala group, assigned to the Lower Pliocene (possibly upper Miocene). The tibiotarsus is fully fossilized and sandy brown in color. A cast of the bone is present in the U. S. National Museum.

*Diagnosis.*—The fossil tibiotarsus is massive, with a rather small condylar head for its shaft diameter. It is characterized by: having a narrow condylar head with a very narrow posterior border of its articulating surface; its narrow intercondylar groove; its very short, papilla-like, external ligamental process; its pronounced internal ligamental prominence; the lack of a definite notch between the intercondylar tubercle and external condyle; and its low, oval distal opening of the tendinal groove.

Measurements: Measurements and their ratios for the fossil are given in Table 1 (see p. 11).

Etymology: The generic name *Dissouroides* reflects the similarity between the fossil tibiotarsus and that of the modern *Dissoura episcopus*. It is a pleasure to name this species in honor of Dr. Loye H. Miller, who has contributed greatly to our knowledge of fossil birds.

#### COMPARISON WITH OTHER FOSSIL STORKS

The fossil tibiotarsus has been compared with descriptions and figures of *Propelargus edwardsi*, *Amphipelargus majori*, *Ciconia maltha*, *Xenorhynchopsis tibialis* and *X. minor*, for which distal tibiotarsi are known.

The following are the known fossil storks from the late Tertiary (mostly taken from Brodkorb, 1963):

Miocene	Pliocene	Pleistocene
<i>Ibis milne-edwardsi</i> —France	<i>Amphipelargus majori</i> —Greece	<i>Ciconia maltha</i> —U. S.
<i>Pelargopappus magnus</i> —France	<i>Ciconia gaudryi</i> —Greece	<i>Xenorhynchus nanus</i> —Australia
<i>Propelargus edwardsi</i> —France	<i>Leptoptilos falconeri</i> —India	<i>Xenorhynchopsis tibialis</i> —Australia

Miocene	Pliocene	Pleistocene
<i>Propelargus</i>	<i>Leptoptilos</i>	<i>Xenorhynchopsis minor</i> —
<i>olseni</i> —Florida	<i>pliocenicus</i> —Russia	Australia
		<i>Leptoptilos titan</i> —Java
		<i>Mycteria wetmorei</i> —U. S.
		<i>Pelargosteon tothi</i> —
		Rumania
		<i>Palaeopelargus nobilis</i> —
		Australia
		<i>Prociconia lydekkeri</i> —
		Brazil

The fossil will be compared below with *Ibis*, *Leptoptilos*, *Ciconia* and *Mycteria*. *Amphipelargus major* (Lydekker, 1891) of the Lower Pliocene from the island of Samos is larger than the present fossil species, and has markedly different tibiotarsal features. Its distal articulating surface projects laterally due to expansion of the anterior inner condyle. This results also in a much wider intercondylar groove than in *Dissourodes milleri*, which shows no notable lateral expansion. The latter also exhibits a much broader supratendinal bridge and an oval, rather than round, distal tendinal groove opening. *Amphipelargus* too differs from *Dissourodes* in possessing a deeper posterior intercondylar sulcus.

*Xenorhynchopsis* of the Australian Pleistocene (De Vis, 1906) differs from *Dissourodes* in the proportionally greater width of the distal end of the tibiotarsus. The condyles are more broadly spaced with a broader intercondylar groove than in *Dissourodes*. The distal opening for the tendinal groove is round and not oval, as in the present species. The major feature of *Xenorhynchopsis* is the presence of a small subpyriform projection at the base of the tubercle lying between the condyles at the distal end of the supratendinal bridge. Unfortunately, the tubercle is broken off near its base in the fossil Nebraska tibiotarsus, but other differences mentioned make it unlikely that *Xenorhynchopsis* is closely related to *Dissourodes milleri*.

The genus *Propelargus* was described by Lydekker (1891) for an Oligocene (or Eocene) and a Miocene species, *P. cayluxensis* and *P. edwardsi*, respectively. A tibiotarsus possibly of the latter species (Lydekker, op. cit., p. 65) was not figured and the description given does not permit detailed comparison with the fossil tibiotarsus. Lambrecht (1933, pp. 318-320) accumulated one complete and four partial distal tibiotarsi assigned to *P. edwardsi*, but the complete one may



represent a juvenile bird. Lambrecht's photograph (p. 319) is not clear, but the tibiotarsus represented shows general resemblance to that of *Dissouroides milleri*. The latter appears to have a more massive shaft, a more pronounced internal ligamental prominence, and an oval rather than round distal opening of the tendinal groove, when compared with the tibiotarsus illustrated by Lambrecht. These differences, the question of identity and age of *Propelargus tibiotarsi*, and occurrence of that genus in French Oligocene to Miocene deposits, seem to preclude its congeneric relationship with *D. milleri*.

The other fossil storks not previously discussed are not represented by tibiotarsi, except for certain species of Recent genera which will be discussed below. *Palaeopelargus nobilis* (De Vis, 1891) was described from metacarpal fragments and appears much larger than *D. milleri* (larger even than *Xenorhynchus*). *Prociconia lydekkeri*, from Pleistocene cave deposits in Brazil, is based on distal tarsometatarsi. It appears to represent a species the size of *Leptoptilos* (sp.), but little can be said about its affinities until we learn more about it. *Pelargopappus* is comprised of three species from the Oligocene (possibly also Eocene) and Miocene of France, and the material includes no tibiotarsi, except for a proximal tibiotarsus of *P. magnus*. The species of *Pelargopappus* were the size of *Ciconia ciconia* (*P. magnus*) or smaller. According to Lydekker (1891, p. 68) *Pelargopappus magnus* shows similarities to *Ibis*. *Palaeohippiorhynchus dietrichi*, an Oligocene stork from North Africa, is not represented by tibiotarsal material. It is apparently closely related to *Ehippiorhynchus* (Lambrecht, 1933, pp. 325-326), a stork approximating species of *Leptoptilos* in size (see discussion of modern forms below). *Ciconiopsis antarctica* was an Argentine Oligocene form and is known only from a metacarpus. Kretzoi (1962) has recently described *Pelargosteon tothi* from the Pleistocene of Rumania. This form was between *Ciconia* (sp.) and *Leptoptilos* (sp.) in size, but no tibiotarsal material is yet available from it.

The tibiotarsus of *Dissouroides milleri* appears to differ considerably from fossil storks represented by tibiotarsal material. Perhaps the greatest need in paleornithology is for comparative osteological studies of modern (and fossil) species, with emphasis on correlating modifications of elements within individual structural complexes and among related structural complexes. Such studies are essential to enable some evaluation of the biology of fossil forms, as well as to enable us better to establish their relationships. The differences between the fossil form and other represented tibiotarsal material

are sufficient to warrant generic distinction for this species. Similarities with fossil species not represented by tibiotarsi remain to be demonstrated.

COMPARISON OF THE FOSSIL WITH LIVING STORKS  
AND THEIR FOSSIL CONGENERS

The following specimens were used in comparison with the fossil tibiotarsus: *Mycteria americana*, 10; *Euxenura galatea*, 2; *Dissoura episcopus*, 3; *Xenorhynchus asiaticus*, 1; *Anastomus lamelligerus*, 1; *Ibis cinereus*, 2; *Ephippiorhynchus senegalensis*, 1; *Ciconia ciconia*, 4; *C. c. boyceiana*, 1; *C. nigra*, 2; *Jabiru mycteria*, 10; *Leptoptilos dubius*, 2; *L. javanicus*, 2; *Sphenorhynchus abdimii*, 1. These species represent all genera listed by Peters (1931). Among living storks *Dissourodes milleri* shows some major similarities with *Dissoura episcopus*, *Jabiru mycteria*, *Ciconia ciconia* and *C. nigra*, and *Euxenura galatea*.

The tibiotarsus of *Dissourodes* differs rather strikingly from *Xenorhynchus asiaticus* in proportions of the condylar head of the bone. In the latter species the head of the bone is deep and narrow, with little evidence of lateral displacement of the inner condyle. The intercondylar groove is proportionally narrower, and the external ligamentary process is much more elongate than that of *D. milleri*. A fossil species, *Xenorhynchus nanus* (De Vis, 1888), is more like *Dissourodes* but is peculiar in the great size of its tendinal groove. The two mycteriine genera, *Mycteria* and *Ibis* (*cinereus*) have the condylar heads of their tibiotarsi shaped generally like *Xenorhynchus* and so differ in a similar manner from the fossil. Their intercondylar grooves are peculiar in being V-shaped anteriorly but sharply shifting to a U-shape near the base of the groove. The distal tendinal groove opening is circular, not oval, in these genera, the species are much smaller than *Dissourodes milleri*, and the latter's tibiotarsus is generally much more massive. *Anastomus lamelligerus* differs from the fossil in many respects including its differently shaped intercondylar notch and shallow anterior condyles, longer supratendinal bridge, round distal opening of the tendinal groove, much more rounded posterior articulating face of the condylar head, and its much smaller size and less massive structure.

Modern species of *Leptoptilos* differ in tibiotarsal conformation from *Dissourodes*. The shaft in the latter is proportionally more massive in relation to the size of its condylar head, although representing a species smaller than those of modern *Leptoptilos*. Fossil

species of this genus include *falconeri* (Lydekker, 1884), *titan* (Wetmore, 1940), and *pliocenicus* (Zubareva, 1948). Of these only *falconeri* is represented by a tibiotarsus that generally agrees with *Leptoptilos* and is quite different from that of *D. milleri*. The supratendinal bridge is shorter in the latter, and the distal opening of the tendinal groove is oval rather than round. The posterior portion of the condylar articulating surface is much broader in *Leptoptilos*. The intercondylar groove is similar in shape in both but broader in *Leptoptilos*. The external ligamental process is ridge-like in *Leptoptilos* and longer, not short and papilla-like. The inner lateral bulge is different in configuration in *Leptoptilos*. Finally, the posterior tip of the inner condylar edge is pointed and sharply angled in the fossil, while it is gently rounded in *Leptoptilos*. These differences are considerable and indicate that that genus is not closely related to *Dissourodes*.

The fossil tibiotarsus is similar in size to that of *Ephippiorhynchus senegalensis*, and its shaft is similar in shape. However, the latter has a very narrow and deep condylar head very unlike that of the fossil. Similarities between *Ephippiorhynchus* and *Dissourodes* include: a narrow intercondylar groove; an unnotched ridge between the intercondylar tubercle and the external condyle; an oval distal opening of the tendinal groove; and, a papilla-like external ligamental process. However, the tibiotarsus of *Ephippiorhynchus* is distinctive in several features, particularly in having a large process flaring anteriorly and laterally from a position beside the proximal opening of the tendinal groove. *Dissourodes* lacks such a process and has a shorter external ligamental process and a more oval distal opening of the tendinal groove. These and other minor configurational differences preclude the fossil being included within *Ephippiorhynchus*.

The modern *Sphenorhynchus abdimii* is much smaller than the species represented by the fossil. There are a number of general similarities between tibiotarsi of the two forms, including: the similarly shaped distal opening of the tendinal groove, the agreement between the two in length and shape of the papilla-like external ligamental process, and the unnotched condition of the ridge between the intercondylar tubercle and the external condyle. Although the distal opening of the tendinal groove is oval in both *Dissourodes* and *Sphenorhynchus*, that of the fossil does not angle laterally and proximally as in *Sphenorhynchus*. The margin of the posterior articulating surface is narrower in the fossil tibiotarsus. The posterior intercondylar sulcus is deeper in the fossil and situated more toward



the inner side, while that of *Sphenorhynchus* resembles *Ciconia* in being shallower and located more centrally. *Sphenorhynchus* exhibits a groove lacking in *Dissourodes*, between the internal ligamental prominence and the anterior face of the internal condyle of its tibiotarsi. Finally the shape of the interior intercondylar fossa of the fossil tibiotarsus is quite different from that of *Sphenorhynchus*. This is chiefly due to the raised area, including the supratendinal bridge and intercondylar tubercle, angling toward the inside of the shaft and *distally* in the fossil tibiotarsus, and toward the inside and *proximally* in *Sphenorhynchus*. These differences are sufficient to preclude very close relationship between *Dissourodes milleri* and *Sphenorhynchus abdimii*.

*Euxenura galatea* approximates the fossil in size of the distal end of its tibiotarsus. The fossil is much more massive than *Euxenura*; indeed the fossil tibiotarsus may be described as having its shaft about the size of *Jabiru*, with a condylar head the size of *Euxenura*. Howard (1942, p. 200) pointed out the ridgelike nature of the external ligamental process in *Euxenura* and *Ciconia* (including the fossil *C. maltha*), in contrast to the papilla found in *Jabiru*. The fossil tibiotarsus resembles that of *Jabiru* (and also *Dissoura episcopus*) in this respect. The fossil tibiotarsus further differs from *Euxenura* in its relatively narrower condyles (both anteriorly and posteriorly), its narrower intercondylar groove (*Euxenura*'s is broad, as in *Ciconia*), in having its intercondylar tubercle connected by an unnotched ridge with the external condyle, and in its longer supratendinal bridge. The distal opening of the tendinal groove is similarly placed in both, although shaped more elliptically in the fossil tibiotarsus. Finally, *Euxenura* agrees with *Jabiru* and *Ciconia* (including *C. maltha*) in having the anterior end of the external trochlea broad and barely indented by the intercondylar depression, rather than narrower and indented as in *Dissoura* and *Dissourodes*.

The fossil tibiotarsus is larger than those of living *Ciconia* species but is approached in size by the fossil *Ciconia maltha* (Miller, 1910). *Dissourodes milleri* differs significantly from *Ciconia* in a number of ways, chief among which are: its narrower intercondylar groove; indentation and narrowing of its anterior external condylar head; its distal tendinal groove opening is oval, not round; the intercondylar tubercle of the fossil tibiotarsus is connected by an unnotched, rather than a deeply notched ridge with the external trochlea; its internal ligamental process is papilla-like, not a long ridge as in *Ciconia*; its condylar head is relatively deeper; its more



pronounced internal ligamental prominence; and, its internal condylar edge is more flaring posteriorly than in *Ciconia*, causing the posterior intercondylar sulcus to be displaced medially (as in *Jabiru*, *Euxenura* and *Dissoura*). The fossil resembles *Ciconia* in having a relatively deep and narrow condylar head.

The massiveness of the fossil tibiotarsus is responsible for some of its similarities with *Jabiru mycteria*. Both have a pronounced internal ligamental prominence, a papilla-like external ligamental process, an unnotched connection between the intercondylar tubercle and external condyle and a flaring margin of the posterior internal condyle. The intercondylar groove, although similar in shape in *Dissouroides* and *Jabiru*, is relatively narrower in the former than in any specimen of *Jabiru* examined. The fossil tibiotarsus has a narrower posterior condylar head than *Jabiru*, and its external ligamental process does not extend as far proximally. The distal opening of the fossil's tendinal groove is oval, not round in shape, and it is not connected by a ridge with the intercondylar tubercle, as in *Jabiru*. Also, *Jabiru* lacks (or has only vaguely present) a process on the supratendinal bridge below the distal opening of the tendinal groove; this process in *Dissouroides milleri* produces a notch above the anterior internal condyle (visible from the internal side).

As has been suggested above, the fossil tibiotarsus most closely agrees with that of *Dissoura episcopus*. The shape of the distal end (viewed end-on) is identical in the two, including the shape of the flaring posterior internal condylar surface, the shape and width of the intercondylar groove, and the relatively narrow posterior margin. The external ligamental process is papilla-like and about equally short in both. The distal opening of the tendinal groove is elliptical in both, and the ridge between the intercondylar tubercle and the external condyle lacks a notch. Although the fossil represents a much larger species, the thickness of the distal shaft and size of the trochlear head are comparable in the two forms. Other similarities include the shape of the condylar margins, depth of the condyles, configuration of the internal ligamental prominence and the angle of the tendinal groove. There are two noteworthy differences between *Dissoura* and the fossil. There is in *Dissoura* a ridge between the distal tendinal groove opening and the intercondylar tubercle. This ridge seems to separate the opening from the rest of the intercondylar fossa. The fossil lacks this ridge and the opening is in direct contact with the deepest part of the fossa. Also, tibiotarsi of the two forms differ in the configuration of the intercondylar fossa. In *Dissoura*

the internal condyle distal to the distal opening of the tendinal groove is more laterally angled. In *Dissourodes* the condyle angles more toward the opening of the tendinal groove, thus reducing the extent of the fossa between the condyle and the opening.

The fossil tibiotarsus thus represents a species related to the modern, paleotropical woolly-necked stork (*Dissoura episcopus*), and probably also the jabiru (*Jabiru mycteria*). While similar to *Dissoura*, *Dissourodes* differs in several respects noted above and in its much larger size and slightly more massive tibiotarsus. Its resemblances to *Jabiru* and its occurrence in the New World warrant generic recognition for this fossil form.

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#### SUMMARY

A fossil tibiotarsus from the Lower Pliocene of Nebraska proves to be a new genus and species of fossil stork, *Dissourodes milleri*. This form differs from all (sufficiently known) fossil and modern storks, but shares many features with *Dissoura episcopus* and also *Jabiru mycteria*. Several differences in the condylar head of the tibiotarsus distinguish it from these two storks.

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TABLE 1

Measurements of *Dissourodes milleri* tibiotarsus

1. Antero-posterior shaft diameter just above external ligamental process. 10.3 mm.
2. Antero-posterior shaft diameter 5 cm. above proximal base of (curvature of) external condyle. 9.4 mm.
3. Antero-posterior shaft diameter 10 cm. above proximal base of (curvature of) external condyle. 10.0 mm.
4. Greatest antero-posterior condylar distance. 21.2 mm.
5. Distance from proximal base of external ligamental process to distal end of the external condyle. 18.5 mm.
6. Distance from proximal base of external ligamental process to proximal base of (curvature of) external condyle. 4.2 mm.
7. Greatest distance across condyles at distal end of tibiotarsus. 16.7 mm.
8. Distance across condyles at internal ligamental prominence. 16.3 mm.
9. Lateral shaft diameter at level of proximal base of external ligamental process. 13.7 mm.
10. Lateral shaft diameter 5 cm. above posterior proximal end of condylar articulating surface. 10.6 mm.
11. Lateral shaft diameter 10 cm. above posterior proximal end of condylar articulating surface. 11.5 mm.
12. Distance across condylar articulating surface at line marking its posterior proximal end. 10.3 mm.
13. Distance across condyles at their anterior ends. 15.6 mm.
14. Distance across anterior intercondylar groove (taken within 1 mm. of bottom of groove). 2.5 mm.
15. Distance from distal opening of tendinal groove to distal, lateral edge of external condyle. 15.4 mm.
16. Distance across supratendinal bridge. 4.8 mm.
17. Distance from a point on the inner (medial) shaft surface at the level of the proximal edge of the supratendinal bridge, to the distal end of the internal condyle. 18.1 mm.
18. Distance across *flat* anterior shaft surface 5 cm. above proximal edge of supratendinal bridge. 8.9 mm.







Three views of the left tibiotarsus of *Dissourodos milleri*, gen. et sp. nov.

From the left, the views are of: (a) the anterior face of the bone; (b) the distal end of the bone, and (c) its inner surface. About  $1\frac{1}{4}$  natural size.









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EMERGED QUATERNARY SHORE LINES  
IN THE MISSISSIPPI EMBAYMENT

By

C. WYTHE COOKE

Honorary Research Associate  
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## CONTENTS

	Page
Introduction .....	2
Fluctuations of sea level.....	4
The tracing of emerged shore lines.....	5
Shore lines along the Atlantic seaboard.....	6
Terraces in Alabama.....	7
Terraces in the Mississippi Embayment.....	8
Morley terrace (shore line 360 feet).....	8
Hazlehurst terrace (shore line 275 feet).....	14
Coharie terrace (shore line 215 feet).....	17
Sunderland terrace (shore line 170 feet).....	23
Okefenokee terrace (shore line 145 feet).....	25
Wicomico terrace (shore line 100 feet).....	27
Penholoway terrace (shore line 70 feet).....	31
Talbot terrace (shore line 42 feet).....	33
Pamlico terrace (shore line 25 feet).....	37
Silver Bluff terrace (shore line 6 feet).....	38
Résumé of events.....	39
References .....	40



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## EMERGED QUATERNARY SHORE LINES IN THE MISSISSIPPI EMBAYMENT

By C. WYTHE COOKE

*Honorary Research Associate  
U. S. National Museum  
Smithsonian Institution*

### ABSTRACT

Borings through the alluvial deposits of the Mississippi Embayment reveal steep-walled valleys entrenched in the underlying Tertiary and Cretaceous formations. Repeated fluctuations of sea level during the Quaternary Epoch drowned the valleys to a maximum height of 360 feet. Emerged shore lines at this and nine lower levels remain horizontal. They stand at the same heights as horizontal shore lines in Alabama and along the Atlantic seaboard. The altitudes of the shore lines and the names of the terraces bounded by them follow:

<i>terrace</i>	<i>altitude in</i>	
	<i>feet</i>	<i>meters</i>
Morley	360	110
Hazlehurst	275	84
Coharie	215	66
Sunderland	170	52
Okefenokee	145	44
Wicomico	100	30
Penholoway	70	21
Talbot	42	13
Pamlico	25	8
Silver Bluff	6	2

Alluvial deposits accumulated at tidal flats and bayhead deltas during each of these ten stages in tidewater that was kept fresh or only slightly brackish by the inflow of the Mississippi and other great rivers that emptied into the bays. At each stage the rivers meandered across the tidal flats built during the preceding higher stages and laid on them a veneer of floodplain alluvium, obscuring but not completely



obliterating the shore lines of the preceding epochs. Thus arose a very gently sloping alluvial plain bordered on each side by more plainly marked terraces.

## INTRODUCTION

The name Mississippi Embayment is applied to a great extension of Cretaceous and younger sediments in the Mississippi Valley and adjacent areas below the vicinity of the mouth of the Ohio River. This includes all of Louisiana, a large part of Alabama, Mississippi, and Arkansas, and smaller areas in Missouri, Tennessee, Kentucky, and Illinois.

The Gulf of Mexico has repeatedly invaded the embayment. The remarkable Upper Cretaceous shells at Coon Creek, Tenn., the Paleocene oysters of the Clayton Limestone, the well-preserved late Eocene shells at Jackson, Miss., and Montgomery, La., the Oligocene fauna at Vicksburg—all give unmistakable evidence of some of those invasions.

Rivers have been flowing into the embayment since Mesozoic time. Their muddy waters played a large part in filling it with sediments. Such formations as the Porters Creek Clay (Paleocene) and the Yazoo Clay (late Eocene) were doubtless built of mud brought down by these rivers.

Quaternary deposits cover a vast area in the Mississippi Embayment. Borings through these sediments prove that before their deposition through-flowing rivers, including the Ohio, the Mississippi, the Ouachita, the White and, the Red, had carved valleys into the older formations of the Coastal Plain, and that these rivers flowed into the Gulf of Mexico somewhere beyond the present coast. The contemporary shore line may have lain not far from the edge of the Continental Shelf (Fisk, 1944, p. 38). Sea level at that time probably lay 400 to 450 feet lower than now (Fisk, 1944, p. 68).

At that early time the Mississippi River flowed west of Crowley Ridge. The Ohio joined it below Natchez, and the Arkansas came in below latitude 30°, near Franklin, La. Later, the Ohio, flowing in a lower valley, captured the Mississippi above Vicksburg, and still later diverted it through Thebes Gap (Fisk, 1944, fig. 45).

These ancient valleys are now buried under a great accumulation of gravel, sand, and silt upon which the rivers now meander with greatly reduced gradients. Fisk (1944, p. 17) estimates that this alluvium "has a volume of approximately 1,000 cubic miles and an average thickness of 132 feet." Krinitzsky (1949, p. 13) increases

the estimate of the volume to 1,200 cubic miles. Fisk (1944, p. 17) assigns all of this alluvium to the Recent Epoch. It seems incredible that this great mass of sediments could have accumulated in the short interval since late Wisconsin time.

Plate 32 and 33 of Fisk's (1944) report place the base of his "Recent Alluvium" in Terrebonne Parish, La., nearly 400 feet below sea level and extend "Quaternary deposits" to approximately -3,500 feet. More recently Druid Wilson (oral communication, 1964) has found well-preserved diagnostic late Miocene marine mollusks in three cuttings from Terrebonne and St. Mary parishes at depths around 2,500 feet. This proves that at least 1,000 feet of Fisk's supposed Pleistocene is really Miocene. The remainder may be Pliocene. His "Recent Alluvium" probably includes the Pleistocene.

Fisk apparently did not include in his estimate of the volume of sediments the terrace deposits bordering the central alluvial plain. He regarded these terrace deposits as fluvial and named them, in ascending order, the Prairie Formation, the Montgomery Formation, the Bentley Formation, and the Williana Formation (Fisk, 1938a, pp. 51, 56, 59, 62). He correlated the four formations with four interglaciations and attributed their present heights above sea level to separate elevations of the land, each of which he conveniently made coincident with a rise of sea level caused by glacial control (Fisk, 1944, p. 69). He supposed that the terraces had been tilted, and he assumed that terraces standing at different heights on the east and west sides of the central plain were of the same age.

Fisk's interpretation of the origin of the terraces in the Mississippi Embayment differs fundamentally from the current interpretation of terraces along the Atlantic seaboard, which explains the terraces as the result of changes of sea level on a stable land.

If the Atlantic Ocean stood higher in past ages, the Gulf of Mexico must have stood at the same height at the same time, and the abandoned shore lines should stand at the same levels in the two regions unless the land has been tilted. If there is a similar sequence of level emerged shore lines in both areas, the assumption is justified that neither has been warped and that there has been no differential change of level between the two areas.

In the present paper an attempt is made to decipher the geologic history of the Mississippi Embayment during the Quaternary Epoch by using the evidence that can be interpreted from topographic maps and to compare it with the results of similar studies along the Atlantic seaboard. Large-scale maps of much of the embayment have been

made by the U. S. Geological Survey, the Mississippi River Commission, and the Corps of Engineers of the U. S. Army. On many of these maps the topography is shown by 5-foot contour lines. On such maps boundaries between terraces can be traced with considerable precision. Because of their great lateral extent and the variation of slope of the land at them, shore lines are much more readily traced on topographic maps than by examination in the field, where the range of view is limited.

#### FLUCTUATIONS OF SEA LEVEL

A dominant cause of emergence and submergence of the land is changes in sea level. Such changes raise or lower the shore line on all islands and continents to the same extent wherever the land has remained stationary. With each change in level the shore line migrates seaward or landward, the distance depending on the slope of the adjacent sea bottom or on the topography of the land.

The Quaternary Epoch was a time of unstable sea level. There appears to have been an intermittent lowering throughout the epoch, reflecting increases in the capacity of the oceanic basins caused by downwarp of the bottom of the sea. There also were variations in the volume of water in the seas resulting from changes in the size of the continental ice caps. During glaciations there was less water in the seas, and sea level was temporarily lower. The resultant of these two causes—glacial control and increase of capacity—was repeated fluctuations of sea level.

As the number of shore lines recognized exceeds the number of generally accepted interglaciations, which were times of high water, some of the shore lines presumably represent intermediate still stands during the intermittent lowering of sea level from causes other than glacial control. The terrace deposits that accumulated during such intermediate stands should lie conformably on the deposits, if any, of the next older terrace, though there might be local unconformities at the lower shore line caused by coastal erosion. The major discontinuities within a sequence of terrace deposits should mark the advance of the sea across the land after each glaciation.

(It should be noted that terrace deposits may be absent from places distant from sources of sediment. A discontinuity at the base of a terrace deposit may indicate merely the lack of sedimentation during the preceding epoch, not erosion.)

Many attempts, none very convincing, have been made to correlate the emerged shore lines with the chronology of the glaciated regions



(Cooke, 1932, 1935; MacNeil, 1950; and others). It is hoped that investigations now in progress in South Carolina (Colquhoun, 1962, 1964) will yield evidence that may point to more definite conclusions.

### THE TRACING OF EMERGED SHORE LINES

Each lowering of sea level, whether caused by expansion of the ice caps or by downwarp of the sea bottom, laid bare a new strip of land; each melting of the ice caps raised the level of the sea and drowned all valleys to the same height. During high stages bayhead deltas accumulated in the drowned valleys; during lower stages trenches were cut by the rejuvenated streams.

The terrace laid bare by the retreat of the sea to a lower stand is not level. It ranges in height from the altitude of the original shore to that of the new. Moreover, it retains all the humps, hollows, and slopes of the original sea bottom except as they may have been modified by the retreat of the sea across them.

The most characteristic feature by which one marine terrace can be distinguished from another is the contemporary shore line. Even that line is not completely level, for it is the mark made on the land by the water, and the location of that mark varies with the force of the waves and the height of the tides. Moreover, the depth of the water at the shore varies from place to place and makes more difficult the recognition of the location of the original surface.

The tracing of an emerged shore line is further complicated by the dissection that it may have suffered since the sea withdrew. In general, the higher, older terraces have suffered more erosion, and their shore lines are the most difficult to trace. However, the relief of the land has more influence on the rate of erosion than its age. A high, wide terrace may be better preserved than a lower, narrower one having greater local relief.

The altitude of an emerged shore line can generally be determined with more precision within an estuary than along the open sea coast, for tidal flats there give a very close approximation to the former sea level. But tidal flats may be restricted to the head of the estuary; farther down the drowned valley the sides may slope steeply into deep water, perhaps even form a vertical bluff. At such places high water may leave little or no mark, or the narrow terrace may later be eroded.

The altitudes assigned to the shore lines in this paper are not precise, but they probably do not differ from the average altitude by more than a few feet, perhaps less than five feet.



The term *marine terrace* as used here includes terraces formed in estuaries as well as those bordering the open sea. A delta built into tidal waters may be considered a marine feature, though it was built by a river, and may rise a few feet above the contemporary sea level. It is the connecting link between a river terrace and a marine terrace.

Shore features and delta deposits may yield the only clues from which the former presence of the sea on the land may be inferred. Clean water drops no clastic sediment. Continuous sedimentation across a large, open bay or far from land in the ocean is not to be expected. Every river and little stream dumps its load of sand or gravel at the shore, from which it is distributed across the bottom by waves and currents. So one need not be surprised to find great areas that must have been submerged beneath the sea completely free from recognizable contemporary sediments or covered by only a thin veneer of sand or silt.

Some geologists deny the marine origin of certain terraces because they find Pliocene or older rocks at the surface within areas claimed to have been flooded during the Pleistocene. They overlook the fact that parts of the Gulf of Mexico off the coast of Florida are floored with bare Eocene limestone (Cooke, 1939, p. 75). Gould and Stewart report outcrops of several other Tertiary limestones in the bed of the Gulf off St. Petersburg and Fort Myers. Dredgings studied by them indicate that "... unconsolidated sediments in many places form only a thin veneer on the bedrock surface, whereas in other areas the bedrock is essentially uncovered" (Gould and Stewart, 1955, p. 13). If the Gulf were to withdraw to a lower level, the newly emerged Recent terrace would be free from terrace deposits at such places.

The names of shore lines and terraces should not be applied to the sediments under the terraces unless there is clear evidence that the sediments are contemporaneous with the shore lines. The geologic formation whose upper surface forms a terrace may be much older than the shore line; if so, the use of the name for those older deposits would not be appropriate. Moreover, the shore line and the terrace are much more extensive than the local geologic unit to which a formation name is applied.

#### SHORE LINES ALONG THE ATLANTIC SEABOARD

Marine terraces were recognized along the Middle Atlantic States as long ago as 1887, when McGee described the Columbia Formation. More detailed work was later done by Shattuck (1901, 1906).

These early workers supposed that the sea had remained stationary while the land rose and tilted. Marine terraces in North Carolina, South Carolina, Georgia, and Florida were later described by B. L. Johnson (1907), Stephenson (1912), Veatch and Stephenson (1911), Matson (1913), Cooke (1924-54), MacNeil (1950), Colquhoun (1962, 1964), and many others. Richards (1962) has reviewed the literature.

A paper on the correlation of coastal terraces (Cooke, 1930b) proposed to define and identify terraces by means of their shore lines. Its abstract (p. 577) states that: "The Pelistocene coastal terraces along the Atlantic Seaboard of the United States are bounded by shore lines that are horizontal south of the glaciated region and that appear to continue unwarped westward along the Gulf coast to Texas." Later work has amply confirmed the essential horizontality of the shore lines along the Atlantic coast; the present work traces the shore lines across the Mississippi Embayment.

Nine terraces have heretofore been recognized along the Atlantic seaboard. To these should be added a tenth, the Morley terrace, herein described. The names of these ten terraces and the altitudes of their shore lines as presently accepted are as follows:

<i>terrace</i>	<i>altitude in</i>	
	<i>feet</i>	<i>meters</i>
Morley	360	110
Hazlehurst	275	84
Coharie	215	66
Sunderland	170	52
Okefenokee	145	44
Wicomico	100	30
Penholoway	70	21
Talbot	42	13
Pamlico	25	8
Silver Bluff	6	2

#### TERRACES IN ALABAMA

Carlston (1950) has traced the terraces from Florida into Alabama, where the coastal terraces are narrower and hence more subject to erosion than at most places along the Atlantic seaboard. He noted (Carlston, 1950, p. 1125) that the estuarine terraces in Alabama are better preserved than those fronting on the Gulf. He recognized scarps at altitudes corresponding to shore lines of the Coharie, Sunderland, Wicomico, Penholoway, and Pamlico terraces and noted another at 145 feet (Carlston, 1950, pp. 1123, 1124) which he tentatively

referred to the Sunderland. This altitude has since been determined as that of the shore line of the Okefenokee terrace. Besides these, remnants of the Hazlehurst terrace are recognizable in Mobile County, and a large part of western Escambia County is occupied by the Morley terrace. The Silver Bluff and the Talbot are well developed on the Coden quadrangle. Thus all ten of the terraces occur in Alabama at the same altitudes as along the Atlantic seaboard. They form the connecting link with those of the Mississippi Embayment, which adjoins them.

#### TERRACES IN THE MISSISSIPPI EMBAYMENT

Above Little Rock, Ark., the Mississippi Embayment is floored by Quaternary deposits that abut the Ozark Escarpment on the northwest and the Mississippi Bluff on the east. The foot of the scarp from Little Rock to Cape Girardeau, Mo., forms a nearly level line very close to 360 feet above sea level. The base of the bluff on the east is lower because the river has cut into the Quaternary deposits, but many remnants of a plain abut the bluff at 360 feet above sea level. I interpret this 360-foot margin of the Quaternary deposits as the shore line of a bay when sea level in the Gulf of Mexico stood 360 feet higher than now.

Other horizontal shore lines of smaller bays can be traced at lower levels. They stand at the same heights above sea level as the shore lines in Alabama and along the Atlantic seaboard. At the heads of several of the bays abandoned deltas rise above the general level.

*Morley terrace (shore line 360 feet).*—The highest inundation reported here backed water in the pre-Pleistocene valleys in the Mississippi Embayment to a height of approximately 360 feet above present sea level. Tidewater then extended up the gorge of the Mississippi probably as far as Gorham, Ill., about 30 miles above Cape Girardeau, which stands at the head of the bay. The valley of the Ohio was flooded for many miles into Illinois and Kentucky. Tidewater may have extended up the Tennessee River to the head of Kentucky Lake (Jeannette, Tenn., quadrangle).

As shown in figure 1, the shore of the bay extended southwestward in a nearly straight line from Cape Girardeau to Little Rock, beyond which it has not been traced. The eastern shore lies high up on the bluff of the Mississippi River and is not so well preserved. It extended past Memphis, Yazoo City, Vicksburg, and Natchez into West Feliciana Parish, La., where the bay opened into the expanded Gulf of Mexico, whose shore extended eastward parallel to the present coast.

Crowley Ridge and other uplands formed a chain of islands from the head of the bay to Helena, Ark.



FIG. 1.—Shore line of the Morley bay.

The name Morley is chosen for the terrace having the 360-foot shore line because the town of Morley, in Scott County, Mo., is built on it not far from the shore. As shown on the map of the Morley quadrangle the entire town stands within a foot or two of 344 feet above sea level. Half a mile north of the city limits



the land slopes gently up to 360 feet, beyond which comes a steep climb to 530 feet. Figure 2 shows the Morley terrace near Benton. Profiles a few miles northwest of Morley are shown in figures 3 and 4.

The Morley terrace is well preserved in the southern part of the Puxico, Mo., quadrangle, where it slopes upward from 325 feet at Ash Hill, Fisk, Lakeview School, and Cypress School to 360 feet at the shore line in sections 21 and 22, T. 26 N., R. 8 E., above which the land rises to 447 feet at Asherville, one quarter mile from the shore. The lower parts of this area appear to have been graded in pre-Morley time by a large river, presumably an early course of the Mississippi. Meander scars of this river pass southwest of Edmunson School and east of Cypress Lateral Ditch No. 1. The divide between this ditch and Lick Creek Ditch stands at 355 feet at Wilkerson School and 357 feet at Dudley.

The western shore of an island in the Morley bay lies near the 360-foot contour line on the Puxico quadrangle, passing 1 mile west of Aid, 1 mile west of Greenwood School, and near Howell School. The island stood 140 feet higher west of Garner School, where the present altitude is more than 500 feet.

The Morley shore line has not yet been traced along the Atlantic seaboard although the terrace is represented there. Much of the area where it occurs is highly dissected and still unmapped. The surface of the Brandywine gravel above 275 feet in Maryland probably forms part of this terrace. Flat areas in South Carolina higher than the Hazlehurst terrace (shore line 275 feet) presumably are remnants of the Morley terrace.

In Georgia, the Morley terrace should be sought in the unmapped area between the Okefenokee Swamp and Tifton, where it probably lies somewhere northwest of the railroad connecting Valdosta with Waycross. The terrace also occupies the eastern part of the Dougherty Plain (Cooke, 1925). The Morley shore line, much eroded, forms the boundary between the Dougherty Plain and the Tifton Upland (Cooke, 1925). It passes about 4 miles west of Sylvester.

A well-preserved plateau around 300 feet extending eastward from Mt. Pleasant, Gadsden County, Fla., and northward into Decatur County, Ga., evidently is the lower part of the Morley terrace unless it is bounded by an unrecognized shore line lower than 360 feet.

A broad plain in western Escambia County, Ala., slopes from 360 feet at the northern edge of the Huxford quadrangle southward across the Atmore quadrangle to 280 feet at the Florida line, a distance



FIG. 2.—Part of the Morley, Mo., quadrangle, 7½-minute series, scale 1:24,000. Contour interval 10 feet. Dotted lines represent 5-foot contours. The shore line of the Morley terrace lies near the 360-foot contour line.



FIG. 3.—Profile on the Advance, Mo., quadrangle from Dongola southeastward to Bird Hill at Perkins.

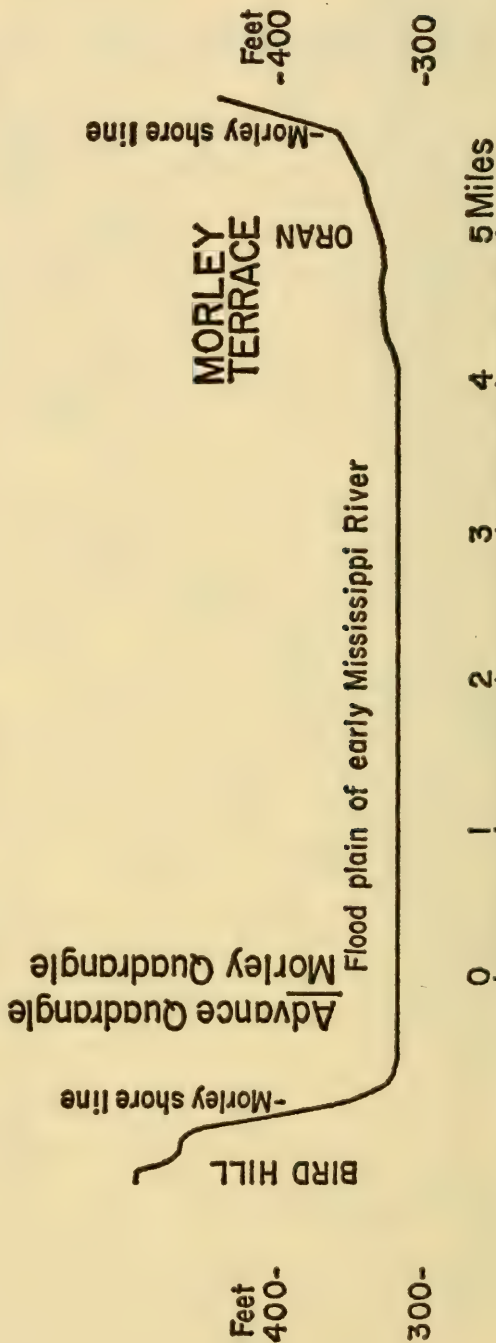


FIG. 4.—Profile from Bird Hill (Advance quadrangle) eastward across the Morley quadrangle to Oran, Mo.



of approximately 18 miles. Dissected remnants occur at least as far east as Murder Creek.

Remnants of a plateau near 340 feet at Citronelle, Mobile County, Ala., extend southward for 5 miles and westward for 4 miles onto the Deer Park quadrangle. The relation of this terrace to the typical Citronelle formation should be investigated.

After a long still stand near 360 feet, sea level receded to about 275 feet above its present location, perhaps without an intermediate drop to a lower level. This caused the emergence of the Morley terrace.

*Hazlehurst terrace (shore line 275 feet).*—The type area of the Hazlehurst terrace (Cooke, 1925, p. 29) is crossed by the road from Hazlehurst, Jeff Davis County, Ga., to Baxley. This plain slopes from about 260 feet to about 215 feet. As there are still no topographic maps of this area, the limits of the terrace have not been determined.

The name Hazlehurst was discarded (Cooke, 1931, p. 505) in favor of Brandywine because the Hazlehurst terrace appears to be the same as one at Brandywine, Md., which had been casually referred to as the Brandywine terrace by Clark (1915, pp. 499, 505) in his description of the Brandywine Formation, an older deposit. Later Cooke (1954, p. 204) revived the name Hazlehurst because that terrace is younger than the Brandywine Formation.

The altitude usually attributed to the shore line of the Hazlehurst ("Brandywine") terrace (Cooke, 1931, p. 505; 1943, p. 104; 1936, p. 130; 1945, p. 248) is 270 feet. A closer approximation is 275 feet.

The Williana terrace of Fisk (1938a, p. 62) may be equivalent to the Hazlehurst terrace, or its type area may be a reduced remnant of the Morley terrace. Fisk chose as its type area the divide followed by the highway from Alexandria to Winfield in Grant Parish, La., 1 mile south of Williana. The altitude there, as shown on the map of the Colfax quadrangle, is about 270 feet. A profile by Fisk (1944, pl. 26) shows part of his supposed Williana terrace well above 500 feet. The correlation is certainly questionable.

The shore line of the largest Hazlehurst bay in the Mississippi Embayment is shown in figure 5. At the 275-foot stage the area covered by tidewater formed a bay more than 100 miles wide at Memphis (fig. 6). Above Helena, Ark., the bay was divided by Crowley Ridge into two long prongs. The western prong reached as far north as the southern parts of Clay and Randolph Counties, Ark.; the eastern prong extended into New Madrid County, Mo., and Lake County, Tenn.





FIG. 5.—Shore line of the Hazlehurst bay.

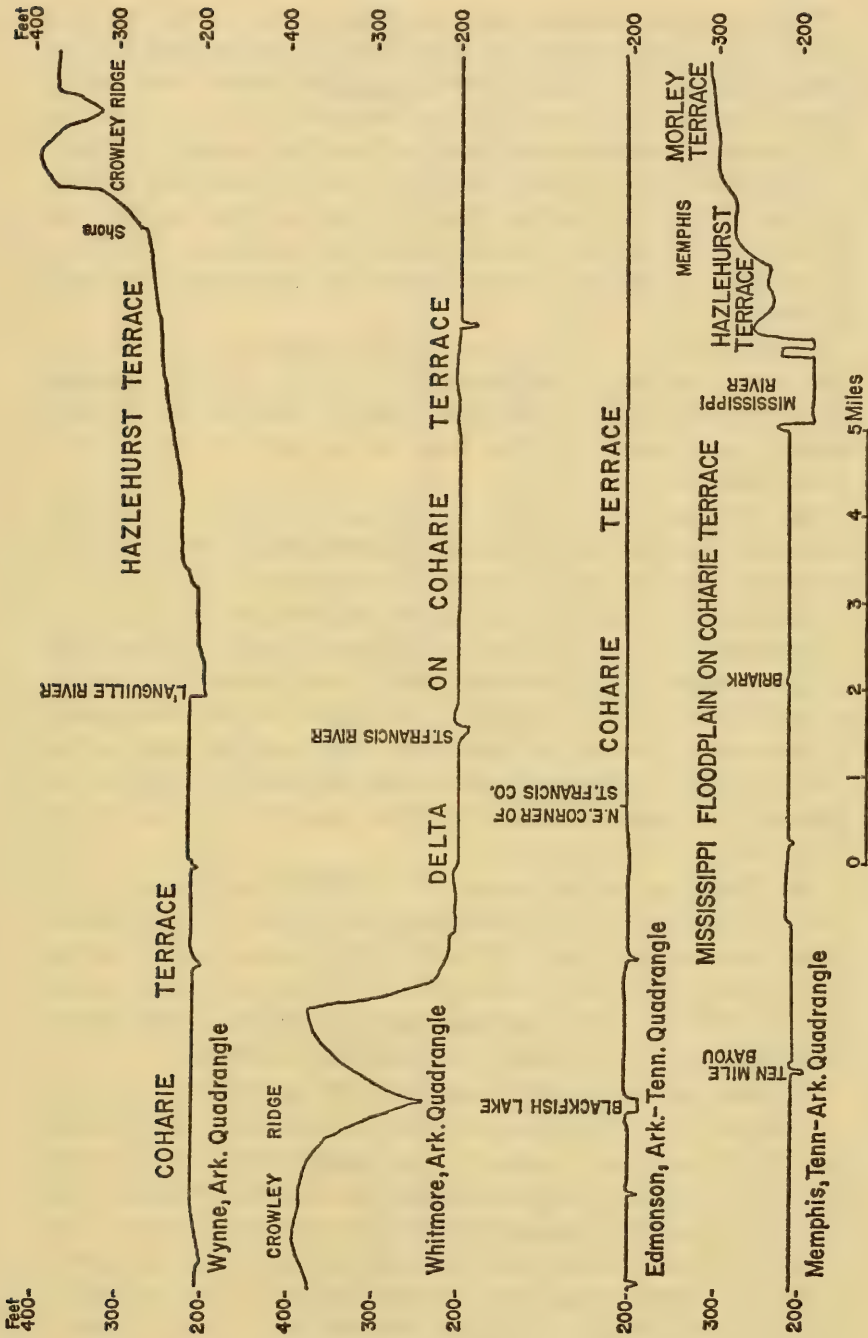


FIG. 6.—Profile from the northwest corner of St. Francis County, Ark., eastward to Memphis, Tenn.

The western shore line followed the bluff as far as Little Rock, not far from the 360-foot shore. It has not been traced in detail beyond Little Rock, but it probably trends southward across Arkansas to Union County, La., thence south-southwestward to Vernon Parish, La., entering Texas somewhere near the thirty-first parallel of latitude.

The eastern shore followed the bluffs across Tennessee and Mississippi to the Gulf of Mexico, whose shore at that stage crossed the northern tier of the West Florida parishes of Louisiana. This shore of the Gulf is difficult to trace because the terrace there is much dissected.

The shore of the Hazlehurst terrace is conspicuous on the Gainesville, Ark., quadrangle. In section 12, T. 18 N., R. 4 E., a broad plain bordering Cache River abuts a steeper slope at the 275-foot contour line. Similar conditions occur on both sides of Jones Ridge, east of Delaplaine.

The 275-foot shore crosses the Marmaduke, Ark., quadrangle, separating the Hazlehurst from the dissected Morley terrace on the northwest. The line passes through Marmaduke and Paragould.

The Hazlehurst shore extends almost due south for 50 miles along the west side of Crowley Ridge, in Craighead County, to Forest Hill in Saint Francis County, following the 275-foot contour line. Part of it near Wynne is shown in figure 6. The opposite shore there is about 50 miles away. That the bay east of the ridge, once the valley of the Ohio, was deeper than the western prong, the original valley of the Mississippi, is shown by figure 7, a profile across the Dee quadrangle in the latitude of Trumann.

The Hazlehurst terrace covers all of the Walnut Ridge, Ark., quadrangle except the northeastern corner, where a short stretch of the shore line is shown. The terrace and the shore extend across the adjoining Powhatan quadrangle, but the terrace slopes gently down to 250 feet at the southern end, following the grade of the drowned valley, and the shore line lies against the bluff.

A drop in sea level caused the emergence of the Hazlehurst terrace.

*Coharie terrace (shore line 215 feet).*—The shore of the Coharie bay (fig. 8) was more crooked. Two prongs near the head were separated by Crowley Ridge and fringes of Hazlehurst terrace. The entrance to the eastern prong, which extended up the drowned valley of the St. Francis River across Poinsett County, Ark., was partly blocked by a 15-mile-long island, the continuation of Crowley Ridge. This prong was roughly triangular, with one shore trending south-

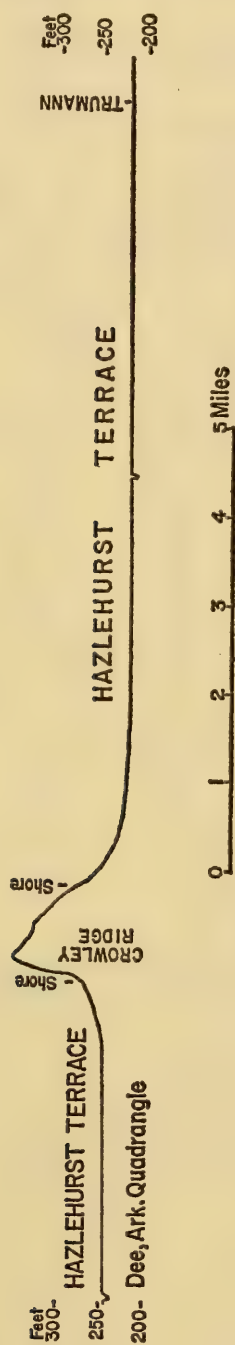


FIG. 7.—Profile across Poinsett County, Ark., from a point 7 miles north of Harrisburg eastward across the Dee quadrangle to Trumann.





FIG. 8.—Shore line of the Coharie bay.

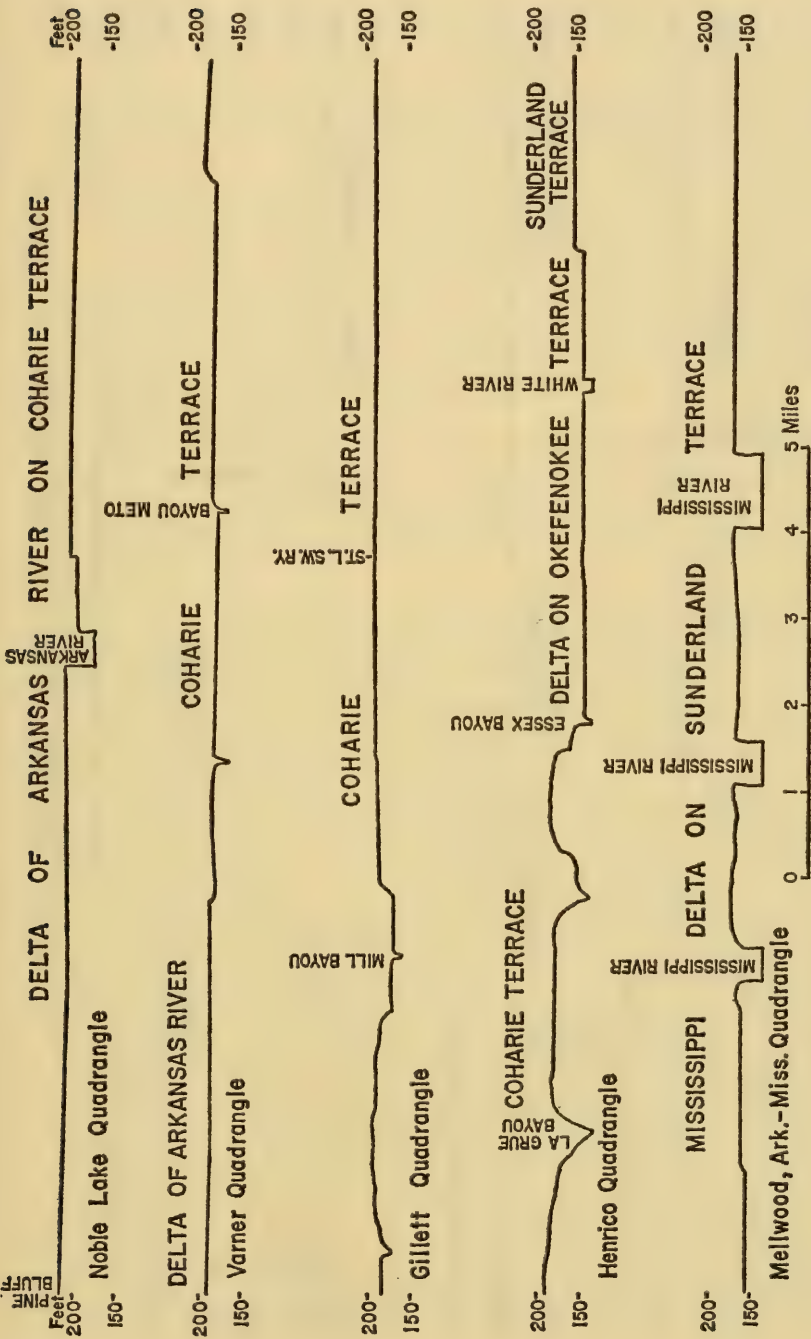


FIG. 9.—Profile extending eastward from Pine Bluff, Ark., into Pinola County, Miss. Part I: Noble Lake, Varner, Gillett, Henrico, and Mellwood quadrangles.

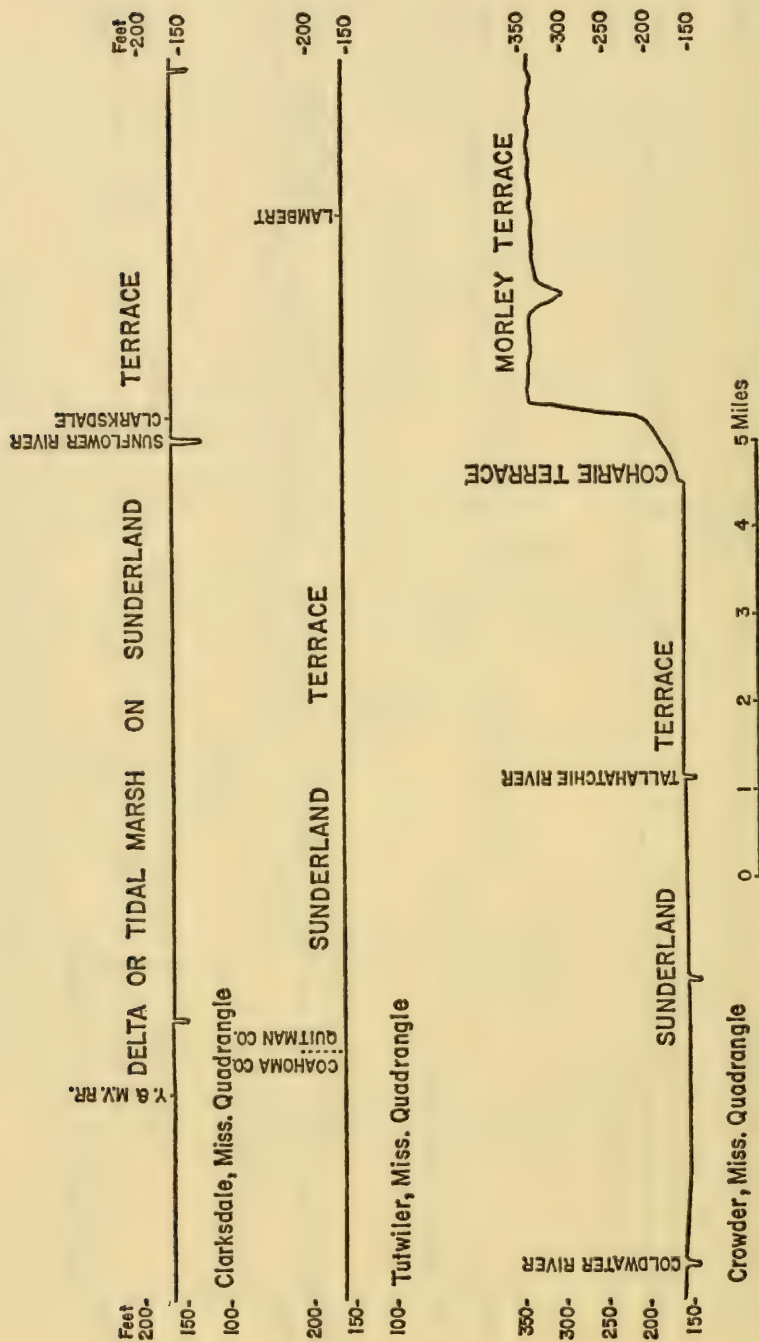


FIG. 10.—Profile extending eastward from Pine Bluff, Ark., into Pinola County, Miss. Part II: Clarkdale, Tutwiler, and Crowder quadrangles.

easterly through Memphis, the other southward almost to Marianna, Ark.

The western prong was roughly rhombic, with one side running from Haynes in Lee County, Ark., to Newport in Jackson County; another side from Newport along the bluff to Higginson, in White County; and another southeastward from Higginson past De Valls Bluff to Monroe County near Roe.

From this cape at the entrance to the western prong, the crooked shore wandered past Stuttgart, Tomberline in Lhoneoke County, and Pine Bluff. From Pine Bluff the shore of the Coharie bay followed the right bank of Bartholomew Bayou about to Warrenton in Lincoln County and thence southward to Paradise in Drew County, which seems a good place to leave it.

In Louisiana the western shore of the Coharie bay has not been traced in detail. It seems to have lain not far west of the Ouachita River as far as Harrisonburg in Catahoula Parish. Here it met the broad entrance to the combined estuaries of Little River and Red River.

The Coharie bay was widest between Pine Bluff, Ark., and Batesville, Miss., a distance of about 120 miles. A profile across it there is shown in figures 9 and 10. Between Harrisonburg and Natchez, Miss., the bay was less than 30 miles wide. The narrow lower reaches of the bay widened to 50 miles between Catahoula Lake and the opposite cape in West Feliciana Parish, La.

From this cape the eastern shore extended northward and north-eastward along the bluffs past Natchez, Vicksburg, and Yazoo City to Memphis, from which the eastern prong crossed into Arkansas.

The shore line at the head of the east prong was very intricate because the old Ohio River (now the Mississippi) and the old Mississippi (now the St. Francis) built deltas across it. Delta building doubtless began while the bay was still flooded and continued after the Coharie terrace emerged. These younger deposits obscure the original shore line in many places, but not everywhere. For instance, at Walnut Grove Corner, near the center of the Dee quadrangle, Ark., a 10-foot scarp rises above the 215-foot level and extends northward for more than 2 miles. Southeast of Harrisburg on the same map the 215-foot contour line hugs the foot of Crowley Ridge. On the Marked Tree quadrangle a distributary of the delta now followed by Little River rises above the 215-foot contour line.

There was also some delta building at the head of the west prong but on a much smaller scale. The old shore line lies at the foot of the



Ozark Escarpment from Bradford (Augusta quadrangle) to the Jackson-Independence County line (Newport quadrangle). Thence it wanders eastward around delta deposits to Bott Spur, 3 miles west of Wynne in Cross County. From this point southward on the Wynne quadrangle there is a low scarp bordering the Hazlehurst terrace, which separates it from Crowley Ridge (fig. 6).

The name Coharie Formation, derived from Great Coharie Creek, a tributary of Black River in North Carolina, was applied by Stephenson (1912, p. 273) to terrace deposits whose upper surface "... forms a terrace plain more or less dissected, which slopes from elevations of about 160 or 170 feet along its southeastern edge to elevations of about 230 or 235 feet along the foot of the escarpment which separates it from the Lafayette belt" (Stephenson, 1912, p. 274). These upper limits are a little too high. The shore line of the Coharie was later placed at 215 feet above sea level by Cooke (1930a, p. 391; 1930b, p. 582; 1935, p. 333; 1936, p. 132), who has traced it through every state from New Jersey to Florida (manuscript maps).

The Coharie terrace is evidently the same as the Bentley terrace of Fisk, which "... slopes southward at a rate of 5 feet per mile from 215 feet above sea level, at the foot of the escarpment near Bentley, to 180 feet at the Grant-Rapides Parish line" (Fisk, 1938a, p. 60). This area occupies part of the combined estuaries of Red River and Little River.

After a long still stand at 215 feet, the sea withdrew to an undetermined lower level and came to rest at or near 170 feet, exposing the Coharie terrace.

*Sunderland terrace (shore line 170 feet).*—At this lower, 170-foot stage of the Gulf, the boundaries (fig. 11) of the lower reaches of the embayment did not differ much in location from the higher stages. Where they had lain near high escarpments only a narrow strip of the Coharie emerged. The greatest changes were in the upper parts of the bay (figs. 9, 10) where the drowned valley was shallower and the drop of 45 feet laid bare a greater width of bay bottom. The shore at the head of the bay became very intricate, for the Mississippi River built a delta, which extended southward from Helena, Ark., almost to Clarksdale, Miss.

An arm of the Sunderland bay extended up the drowned valley of White River to a head above Clarendon, Ark. Its mouth at St. Charles in Arkansas County was about 12 miles wide. Another branch



FIG. 11.—Shore line of the Sunderland bay.

headed in Lincoln County, Ark., between Meroney and South Bend, where the delta of the Arkansas River was 20 miles wide.

Outside of the Mississippi Valley, another long, narrower bay extended up the drowned Red River Valley from Alexandria, La., to a head above Shreveport.

The bayous in western Arkansas County and eastern Jefferson County in Arkansas occupy former tidal marshes whose shore follows the 170-foot contour line on the Gillett quadrangle. A 10-foot scarp 3 miles southwest of Gillett leads up to the Coharie terrace.

The name Sunderland terrace dates from 1901, when it was proposed by Shattuck (1901, p. 102). The name is taken from a hamlet in Calvert County, Md. As described by Shattuck the Sunderland is a marine terrace having a shore line about 170 feet above sea level. In later work Shattuck (1906, p. 68) included parts of several terraces in the Sunderland, which he thought had been warped. According to Cooke (1931, p. 507) "The name Sunderland should be restricted to the terrace that is bounded by the shore line at or near 170 feet above sea level."

The Sunderland appears to be the same as Fisk's (1938a, p. 56) Montgomery terrace, which lies within a former estuary of the Red River. The type locality of this terrace is at the intersection of U. S. Highway 71 and State Highway 162 near Montgomery, Grant Parish, La. The altitude of this intersection as shown on the map of the Montgomery quadrangle is approximately 170 feet above sea level. The 20-foot contour interval on the map is too great to show the exact location of the shore line.

The withdrawal of the Gulf from 170 feet to a lower level drained the flooded valleys and exposed the Sunderland terrace.

*Okefenokee terrace (shore line 145 feet).*—The approximate location of the shores of the Okefenokee bay is shown in figure 12. At the 145-foot stage the Mississippi Valley was drowned as far north as the thirty-fourth degree of latitude, that is, to Tallahatchee and Bolivar counties in Mississippi. In Arkansas tidewater extended up the White River even farther north, to the vicinity of St. Charles. The western shore of the estuary through Arkansas was fairly straight between St. Charles and the Louisiana border. Below Selma, in Drew County, it lay west of Bartholomew Bayou. In Louisiana it followed the western side of the Ouachita Valley as far as Harrisonburg, beyond which it passed southwestward to the Gulf of Mexico. A profile across the Okefenokee terrace at Bastrop, La., is shown in figure 13.



FIG. 12.—Shore line of the Okefenokee bay.



The Okefenokee shore is very conspicuous on the map of the Collins, Ark., 7½-minute quadrangle, where it is separated from the adjoining Sunderland or Coharie terraces by a 30-foot scarp. It nearly coincides in location with the Sunderland beach, which seems to have been cut away locally by stream erosion.

The contact with the Sunderland terrace, here very narrow, is shown on the Philipp, Miss., quadrangle along the foot of the bluff between Paynes, Tallahatta County, and Oxberry, Grenada County, where it is marked by the 145-foot contour line.

The Okefenokee terrace takes its name from the Okefenokee Swamp in southeastern Georgia and adjoining Florida, which is its most distinctive feature. Otto Veatch (Veatch and Stephenson, 1911, pp. 35, 36) described the "Okefenokee plain" as "a wave-built, marine terrace, recently raised above sea level." "Perhaps 125 feet" is the highest altitude assigned to it by Veatch. MacNeil (1950, pp. 99, 102) referred the terrace to a shore line near 150 feet. A closer approximation is 145 feet.

*Wicomico terrace (shore line 100 feet).*—The shape of the Wicomico bay is shown in figure 15. At the beginning of the 100-foot stage the Mississippi Valley was flooded for several miles above the Louisiana line into Arkansas. The shallow head of the bay became silted up by the muddy river, and distributaries of a delta pushed southward nearly 30 miles into Louisiana. The delta ended near Epps in Carroll Parish (Mitchiner quadrangle) in water about 20 feet deep.

Along the Ouachita Valley tidewater extended 50 miles beyond the state boundary as far as Camden, Ark., where the present floodplain covers the Wicomico terrace. On the Moro Bay quadrangle a low scarp passing Ebenezer School separates the Wicomico terrace from a low part of the Okefenokee terrace. A much higher scarp adjoins the Wicomico south of the river.

The 100-foot contour line lies near the bottom of a high bluff from Twin Oaks on the Bastrop quadrangle to Collinston on the Collinston quadrangle. The Wicomico terrace extends from this line eastward beyond the limits of the quadrangles (fig. 13). It slopes very gently southward and merges into the Penholoway terrace near Collinston.

In Union Parish, La., patches of Wicomico terrace border the uplands west of the Ouachita, notably at Litroe and Gravel (Haile quadrangle). Farther south, in Ouachita Parish, there are areas west and south of Monroe. Beyond these the Wicomico shore lay close to the Ouachita River to Harrisonburg, where it turned southwestward to the mouth of the Red River estuary below Alexandria.

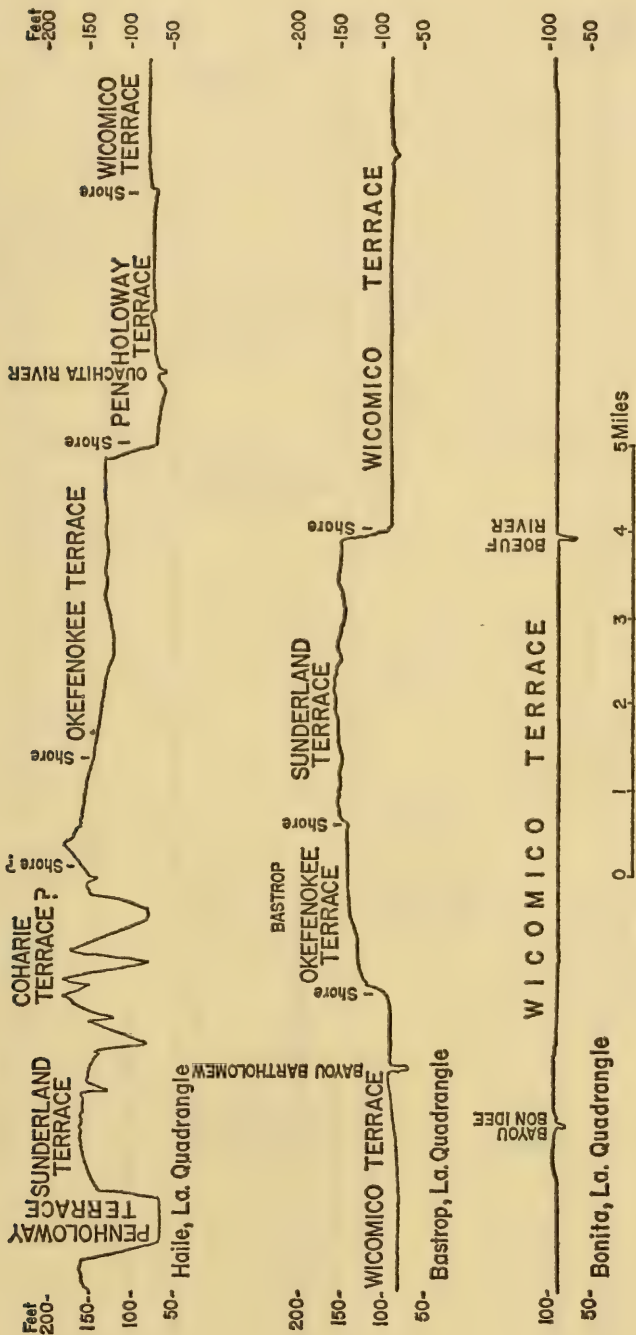


FIG. 13.—Profile from a point 10 miles south of Marion, Union Parish, La., eastward to Yazoo County, Miss. Part I: Haile, Bastrop, and Bonito quadrangles.

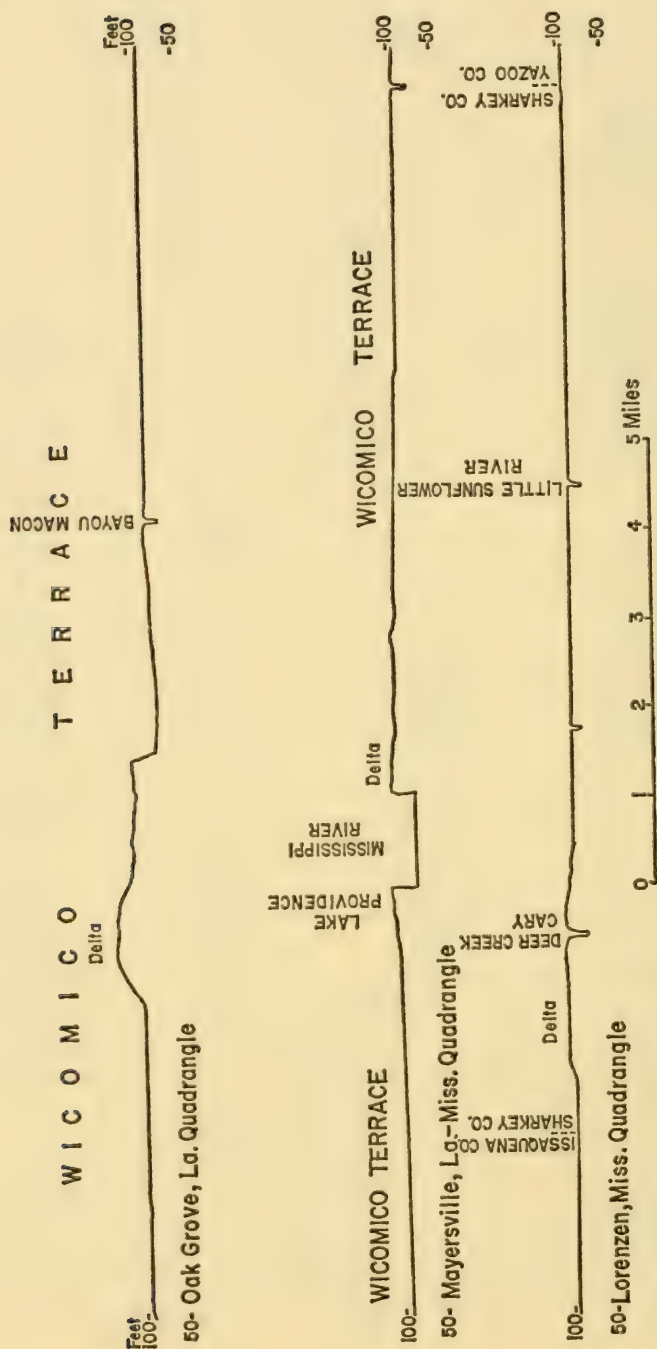


FIG. 14.—Profile from a point 10 miles south of Marion, Union Parish, La., southward to Yazoo County, Miss. Part II: Oak Grove, Mayersville, and Lorenzen quadrangles.



FIG. 15.—Shore line of the Wicomico bay.



Bayou Bartholomew flows upon the Wicomico terrace at Bastrop, where it adjoins the Okefenokee terrace. Four miles east of Bastrop the Wicomico abuts the Sunderland terrace, from which it extends eastward into Mississippi (figs. 13, 14).

In Mississippi the head of the Wicomico embayment is masked by distributaries of the contemporary Mississippi delta. Parts of the terrace occupy the eastern part of the Swan Lake quadrangle and much of the adjoining Auter quadrangle in Washington, Humphreys, and Sharkey counties (fig. 14). From Yazoo City southward the shore followed the bluff into Louisiana. At a low cape 3 miles southeast of Port Hudson, East Baton Rouge Parish, the shore turned eastward along the expanded Gulf of Mexico.

The name Wicomico terrace dates from 1901, when Shattuck (1901, p. 103; 1906, p. 71) applied it to a marine terrace in Maryland whose shore line now stands about 100 feet above sea level. The name has been used repeatedly since then for all the states from Maryland to Florida.

Fisk's (1938a, p. 51) name Prairie terrace evidently is a synonym of Wicomico terrace. The name was "proposed for a terrace typically developed near Aloha, sec. 16, T. 7 N., R. 4 W., Grant Parish, and at Nebo School, irregular sec. 40, T. 7 N., R. 3 E., La Salle Parish" in Louisiana. At Aloha (Montgomery quadrangle) and also at Nebo School (Jena quadrangle) this plain is bounded by the 100-foot contour line. Aloha lies within the Wicomico estuary of the Red River about 6 miles above Colfax; Nebo School stands on the shore of the wide entrance to a larger Wicomico bay about 23 miles southwest of Harrisonburg.

The Port Hickey terrace of Matson (1916, p. 190) as defined by Fisk (1938b, p. 8) is here interpreted as equivalent to the Wicomico. It slopes up from more than 90 feet above sea level at Port Hickey (Port Hudson quadrangle) to 100 feet at Port Hudson, a mile and a half away.

MacNeil (1950, p. 99) regarded the Wicomico as a peak of marine transgression. This assumption seems to be corroborated by Colquhoun (1964, p. 137), who finds the Okefenokee Formation to be overlain unconformably by Wicomico terrace deposits in the Eutawville quadrangle of South Carolina.

At the end of Wicomico time the Gulf withdrew to a lower level and came to rest at 70 feet.

*Penholoway terrace (shore line 70 feet).*—At the 70-foot stage a bay about as long as Chesapeake Bay and more than twice as wide



FIG. 16.—Shore line of the Penholoway bay.

extended across Louisiana into Arkansas (fig. 16). An eastern prong reached up Tensas Bayou into Madison Parish, La. The upper part was bounded on the east by the delta of the Mississippi, which pushed down below Grand Gulf, Miss. The western shore lay west of Bayou Macon. This eastern prong was separated from the drowned valley of the Ouachita by a low-lying peninsula of Wicomico terrace that extended southward beyond Leland into Catahoula Parish.

The western prong of the Penholoway bay forked near Monroe, La. One wide branch followed Bayou La Fourche almost to Collins-ton; the other pushed up the Ouachita into Arkansas beyond the mouth of the Saline River, with a narrow place near the town of Ouachita, in Union Parish. Tidewater also reached up Bayou d'Arbonne and Bayou l'Outre.

At Harrisonburg the shore turned southwestward along the highland west of Bushley Creek and Catahoula Lake, where it curved southeastward to the expanded Gulf of Mexico in Avoyelles Parish near Long Bridge.

In the western part of Evangeline Parish the shore of the Gulf followed the boundary line between the "Montgomery Formation" and the "Prairie Formation" as mapped by Varvaro (1957, pl. 1). Presumably, therefore, the "Prairie terrace deltaic surface" of Varvaro (1957, p. 37) is equivalent, at least in part, to the Penholoway terrace.

The eastern shore of the Penholoway bay lay not far east of the Mississippi River from Grand Gulf, Miss., to a projecting cape at Alsen, about 4 miles north of Baton Rouge, where it met the Gulf.

The State Industrial School for Boys at Alsen (Scotlandville, La., quadrangle) is built on the Penholoway terrace near the shore of a cove that curves eastward past Baker, which stands on the Wicomico terrace just above the Penholoway shore (fig. 17). The greater part of the city of Baton Rouge is built on the Penholoway terrace, but the southern part steps down to lower terraces (fig. 18).

The Penholoway terrace was named by Cooke (1925, p. 24) from Penholoway Creek and Penholoway Bay (a swamp) in Georgia. It was further defined by reference to a shore line at 70 feet (Cooke, 1931, pp. 505, 509). It has been mapped in Georgia (Cooke, 1939b, 1943), South Carolina (Cooke, 1936), and Florida (Cooke, 1945).

After the sea withdrew from the 70-foot level it came to rest at 42 feet.

*Talbot terrace (shore line 42 feet).*—During the 42-foot stage of the Gulf (fig. 19) the mouth of the Talbot bay lay between Baton



FIG. 17.—Profile on the Scotlandville, La., quadrangle extending northward from the Thomas Road at North Maryland.

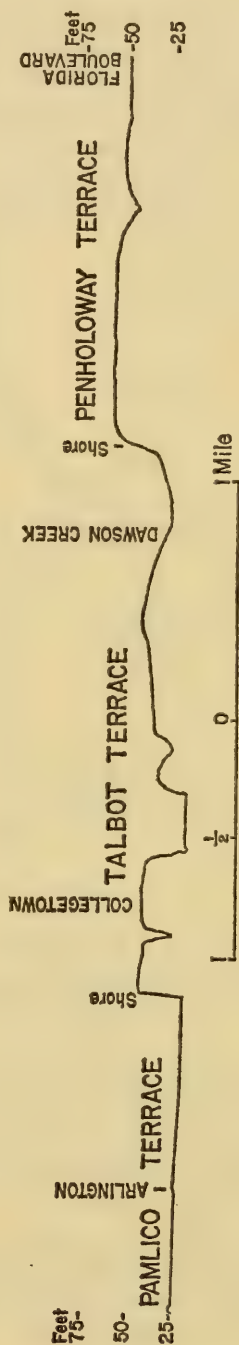


FIG. 18.—Profile on the Baton Rouge West, La., quadrangle extending from Arlington to Florida Boulevard at Foster Drive.



Rouge and Lafayette, La., a width of 40 miles. The shore line at Baton Rouge (fig. 18) crossed the intersection of the Kansas City Southern Railway with the St. Helena Meridian as shown on the Baton Rouge West quadrangle. From this point a 10-foot scarp extends eastward past the Baton Rouge Country Club.



FIG. 19.—Shore line of the Talbot bay.

West of the cape at Lafayette the shore of the Gulf was very low lying; there is no conspicuous scarp separating the Talbot terrace from the Penholoway. The shore line appears to curve northward past Cankton (Carencro quadrangle) to the south corner of Church Point.

Within the bay, whose generalized outlines are shown in figure 19, the shore line is made very intricate by distributaries of the Red River delta now occupied by Bayou Cocodrie, Bayou Boeuf, Bayou Rouge, and other bayous. Traces of the original level can still be

seen at St. Landry (Turkey Creek quadrangle) and at many places within the Bunkie quadrangle.

Water backed up Little River for several miles above Catahoula Lake, which now is blocked by delta deposits. The Talbot bay extended up the Mississippi Valley at least as far as Dismal Swamp (Deer Park quadrangle) in Concordia Parish.

The name Talbot terrace dates from 1901, when Shattuck (1901, p. 103) applied it to a marine and estuarine terrace in Maryland having a shore line near 45 feet above sea level. It is the same as



FIG. 20.—Shore line of the Pamlico terrace in Louisiana.

the terrace in North Carolina later called Chowan by Stephenson (1912, p. 328). The terrace has also been described and mapped in South Carolina (Cooke, 1936a) and Georgia (Cooke, 1939b; 1943). The upper level of the "Pensacola terrace" of Matson (Matson and Sanford, 1913, p. 34; Cooke, 1939a, p. 40) is equivalent to the Talbot terrace.

When the sea withdrew from the Talbot terrace to an undetermined lower level it came to rest at 25 feet.

*Pamlico terrace (shore line 25 feet).*—The generalized outlines of the Pamlico shore in Louisiana are shown in figure 20. The capes at the mouth of the largest Pamlico bay stood near Hope Villa,

14 miles southeast of Baton Rouge, and at Delacroix, 3 miles southeast of St. Martinville. The entrance to the bay was more than 50 miles wide. The head of the bay lay in St. Landry Parish near Elba and in Pointe Coupee Parish near Morganza.

In the western part of the bay drainage from the Red River built a long delta, now followed by Bayou Teche, from Port Barre past Leonville and Arneaudville to Breaux Bridge. Drainage from the Mississippi built a delta down the middle of the bay along the Atchafalaya past Melville to Krotz Springs. Another distributary followed Bayou Fardoche from Morganza to Frogmore on Bayou Grosse (Fardoche quadrangle), and wider branches bordered the river from Morganza to the southeast corner of the New Roads quadrangle.

The western shore of the Pamlico bay follows the 25-foot contour line on the Carencro quadrangle for 6 miles, passing 3 miles east of Sunset. Here it lies at the foot of a 30-foot bluff leading to the Penholoway terrace.

Most of the bay appears to have been shallow. It probably did not much exceed 25 feet in depth.

The name Pamlico Formation was used by Stephenson (1912, pp. 286, 287) for Pleistocene beds along Pamlico Sound in North Carolina ". . . whose upper surface forms a low, nearly level plain whose elevation nowhere exceeds 25 feet." The plain was called "Pamlico terrace" on an earlier page of the same volume, by William Bullock Clark, whose description was based on Stephenson's field work. The Pamlico terrace has been mapped in all the states from Maryland to Florida.

At the end of the still stand at 25 feet the Gulf withdrew and came to rest about 6 feet above its present level. The Pamlico terrace emerged.

*Silver Bluff terrace (shore line 6 feet).*—The name Silver Bluff was substituted (Cooke, 1945, p. 248) for the name Miami terrace (Parker and Cooke, 1944, p. 24) to avoid confusion with the Miami Oolite, which is older.

At the 6-foot level the present salt marshes along the Gulf were completely submerged. A bay occupied the drowned drainage system of the Atchafalaya as far north as Catahoula (Loreauville quadrangle), about 10 miles northeast of St. Martinville and Crescent (Chicot Lake quadrangle). At the White Castle Oil field (White Castle quadrangle) it was stopped by the delta of the Mississippi, which formed its eastern boundary.

In many places the shore at the 6-foot stage was so low that it cannot be traced on maps with a 5-foot contour interval. An exception is at Ponchatoula, where a bluff rises about 10 feet above the 5-foot contour line, which bounds the marshes north of Lake Marepas. This bluff continues westward into the Springfield, La., quadrangle.

The shore of the Gulf during Silver Bluff time is marked by a narrow barrier beach, rising 10 feet above the 5-foot line, that curves across the southwestern part of the Lake Charles quadrangle. Grand Lake School, in sec. 16, T. 12 S., R. 8 W., stands on it.

#### RESUME OF EVENTS

At the beginning of the story, presumably in Pliocene or early Pleistocene time, the shore of the Gulf lay beyond the present sea-shore, and rivers flowed across the Mississippi Embayment in steep-walled valleys carved in bedrock. Then, perhaps during the first interglaciation, the sea rose and flooded the embayment to a height of 360 feet above its present level.

This inundation produced a great bay extending about 250 miles northeastward from Little Rock and averaging about 100 miles in width. Later, the Gulf established shore lines successively near 275 feet, 215 feet, 170 feet, 145 feet, 100 feet, 70 feet, 42 feet, 25 feet, and 6 feet. There were probably intermediate lower stands whose locations have not been established. At each level the drowned valleys formed successively smaller bays.

In each bay the rivers deposited their load of sediment not far from the shore, filling up the head of the bay and usually extending distributaries of a delta into deeper water. These distributaries were abandoned when sea level fell to a lower level. At the present stage the embayment is completely filled and the Recent delta bulges out into the Gulf.

Thus developed a series of terraces bordering a very gently sloping area across which the once-rapid streams now meander. The old shore lines within the central area are masked by veneers of alluvium except where distributaries of Pleistocene deltas, their channels now occupied by minor streams, stand above the general level.

Objection will doubtless be raised to this theory of the growth of the terraces and the alluvial plain of the Mississippi Embayment because the sediments appear to be fluvial deposits. They have every right to look like fluvial deposits, for they were brought down by rivers, dropped for the most part as tidal flats and deltas in water that



was kept fresh or only slightly brackish by the great volume of river water flowing into the bays.

Even the largest bay must have been nearly fresh, for it received all the drainage from the midcontinent. Into the head of the bay flowed the Tennessee, the Ohio, and the Mississippi. No large streams came in from the east, but the western side received the St. Francis, Spring River, Strawberry River, the White, the Little Red, and the Arkansas. These large streams must have kept the Morley bay nearly fresh as far down as Little Rock. Later, smaller bays were only slightly brackish as far south as Natchez, at which latitude the pre-Pleistocene valleys were narrowed by uplands west of Harrisonburg, La. South of Harrisonburg the sea water was diluted by the Ouachita, Little, and Red Rivers. Clearly, lack of sea shells is no evidence that the Quaternary deposits of the Mississippi Embayment did not accumulate in tidal waters.

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# ADDITIONAL DATA ON THE HOST RELATIONS OF THE PARASITIC COWBIRDS

By  
HERBERT FRIEDMANN

*Director, Los Angeles  
County Museum of Natural History*

Publication of my 1963 book (see bibliography) on this subject prompted a number of observers to send me their records of the two North American species of cowbirds, the brown-headed and the bronzed, with the request that I bring out a supplement to it. To this data I have added a few recently published records to make the present paper as useful as possible. In all cases the reader should consult my 1963 book for full data.

## Brown-Headed Cowbird

*Molothrus ater*

The hosts of this wide-ranging cowbird now include two new species, one of which, the spotted sandpiper, can only be looked upon as an "accidental" victim. (Occasional additions to the list of ill-adapted hosts do occur but are without biological significance. They mean only that a cowbird with an egg to be laid may lay it in an unsuitable nest if a suitable one is not available.) A real, but by no means new, problem is raised by new data on Bell's vireo and the cardinal as cowbird hosts: how to treat quantitatively with statistical significance rapidly and unevenly changing total blocks of record data while maintaining a relative appraisal among the frequently victimized fosterers. No workable solution to this difficult question has yet been found.

For many years I have been trying to interest biometricians in the problem of estimating the quantitative aspects of the host-parasite relationship in many of the frequent fosterers, but the number of variables has discouraged the few who even began to survey the problem. Scott's recent data on the cardinal, discussed below, has caused,



in the light of earlier knowledge, such a major reevaluation of this particular host with respect to the parasite that it may be cited as further justification of the reluctance of the biometricians. The data on Bell's vireo presented in this paper is another case in point. With the recently renewed interest in the total complex of problems surrounding the parasitic breeding biology of the cowbirds (see Wiens, 1963, and Young, 1963), it is possible that some sound quantitative evaluation of this situation may be forthcoming.

### Spotted sandpiper

*Actitis macularia* (Linnaeus)

This bird may be added to the list of "freak" cases of cowbird parasitism. Turner (1964, p. 518) reported finding a nest of this sandpiper containing one cowbird egg (*M. a. artemisiae*) at Edmonton, Alberta.

### Dusky flycatcher

*Empidonax oberholseri* Phillips

This little known species is an addition to the known hosts of the brown-headed cowbird (subspecies *artemisiae*). J. Stuart Rowley (in litt.) collected a nest containing two eggs of the dusky flycatcher and one of the cowbird at Virginia Lakes, Mono County, California, on June 19, 1940.

### Black-capped chickadee

*Parus atricapillus* Linnaeus

Another instance of cowbird parasitism on the nominate race of this chickadee was recorded by Root (1961, p. 43) from North Andover, Massachusetts, July 15, 1961. It involved a fledged cowbird repeatedly fed by a black-capped chickadee.

### Wrentit

*Chamaea fasciata* (Gambel)

T. R. Howell observed a young fledgling cowbird repeatedly fed by a wrentit at Pacific Palisades, Los Angeles, July 27, 1963. The record refers to the race *henshawii* of the host and *obscurus* of the parasite. The increase in the cowbird population in southern California will probably make the wrentit a fairly common victim of its parasitism.

### Bushtit

#### *Psaltiriparus minimus* (Townsend)

On July 14, 1963, at Los Angeles, T. R. Howell examined a deserted nest of a bushtit that contained a mummified carcass of an almost fledged bushtit, part of a shell of a bushtit egg, and about one-half of the shell of a cowbird egg (*M. a. obscurus*). The last had a yellow crusty inner coating of dried yolk and presumably did not hatch.

### Ruby-crowned kinglet

#### *Regulus calendula* (Linnaeus)

Another instance of cowbird parasitism on this infrequently used host has been reported. At Virginia Lake, Mono County, California, 9,400 feet, a pair of these birds was seen feeding a fledged young cowbird (race *artemisiae*) (Shepard, 1962, pp. 505-506). This is the second time this host has been reported rearing the young of the parasite.

### Mockingbird

#### *Mimus polyglottos* (Linnaeus)

Although the mockingbird had been reported as an infrequent victim of the brown-headed cowbird in a number of areas, it was never found to rear the young parasite. Recently Webster (1964) reported that Dr. Pauline Jones found this host (race *leucopterus*) rearing a young cowbird (*obscurus*) in southern Texas.

### Cedar waxwing

#### *Bombycilla cedrorum* Vieillot

The cedar waxwing has been parasitized relatively infrequently, but in July of two successive years, 1964 and 1965, four parasitized nests were found in or near Waterloo County, Ontario, Canada, by Mr. Robert Pickering. Each contained one egg of the brown-headed cowbird and four of the host. The unusual incidence of parasitism is seen in proper perspective when we recall that in a fairly similar locality in southern Quebec, Terrill found four parasitized nests (out of a total of 329 waxwing nests examined) during a period of 50 years. Dr. Johan Ottow told me of the new cases, which bring the total number of records from 18 to 22.

### Black-capped vireo

*Vireo atricapilla* Woodhouse

Graber's study (1961) greatly extends our knowledge of this vireo. She reported on 76 nests in which a total of 243 vireo eggs were deposited. Of these, 134, or 55.1 percent, were lost before hatching, and of these 134 Graber considered cowbird parasitism accounted for 97, or 72.3 percent. In addition, eight vireo chicks were lost because of the presence of cowbird chicks in the nests. The percentage of parasitism of the 76 nests is not given, but it must have been considerable as Graber wrote that, ". . . during the nestling period, as during laying, the chief loss was due to cowbird parasitism. In all cases in which a cowbird chick occupied the nest, no vireo chicks survived. . . ."

### Bell's vireo

*Vireo bellii* Audubon

Additional data on this frequent victim of the cowbird is included only to emphasize the statistically unsatisfactory nature of present methods of evaluating the quantitative aspects of host-parasite relations. In my 1963 summary (pp. 84-85) I noted some 82 instances of cowbird parasitism on Bell's vireo, but added ". . . these constitute only a fraction of the number that lie back of the numerous estimates put forward by various authors . . ." (i.e., authors who explicitly mentioned a number of instances but added loose statements to the effect that the vireo was victimized far more frequently in their area). Since then I have learned of nearly half as many cases more, no less than 28 from two papers alone (Ely, 1957, unpublished thesis; Overmire, 1962). The increase is not a measure of any change in the relationship between the vireo and the cowbird but merely an indication of additional observation and more increments to the recorded data.

### Dwarf vireo

*Vireo nanus* Nelson

Three more cases of parasitism of this vireo at Irapuato, Guanajuato, Mexico, have been found in the Moore collection by Dr. J. W. Hardy. These, and the one noted in my 1963 book (p. 83), were found within one week, June 17 to 26, 1943, indicating a high frequency of parasitism locally.

### Swainson's warbler

*Limnothlypis swainsonii* (Audubon)

To Kirn's 1917 record of this warbler as a cowbird host in Copan County, Oklahoma (Friedmann, 1963, p. 92), Vaiden (1962, p. 2) added a second instance, found in Bolivar County, Mississippi, and in 1963 still another in Mississippi. He suggested that the Swainson's warbler may prove to be a regular and not infrequent host of the cowbird in the area around Rosedale, Mississippi.

### Grace's warbler

*Dendroica graciae* Baird

On June 30, 1954, near the Grand Canyon village, south rim of Grand Canyon, Arizona, George A. Hall (in litt. March 11, 1964) observed a pair of Grace's warblers feeding a fledged young brown-headed cowbird (*M. a. obscurus*).

### Golden-cheeked warbler

*Dendroica chrysoparia* Sclater and Salvin

Warren M. Pulich (1965, p. 548) reported that of 19 nests examined by him in a 70-acre tract in the Edwards plateau country of Texas, 15 were found to contain eggs or young of the cowbird. He also had at that time seven other records in addition to the nine listed in my 1963 account.

### Cardinal

*Richmondia cardinalis* (Linnaeus)

The status of the cardinal as a cowbird fosterer varies greatly in different parts of its range, much more than in most host species. The recent study of Scott (1963) in the vicinity of London, Ontario, presents the most extreme situation yet recorded, with an incidence of parasitism of over 60 percent and a greater number of instances (113) than previously known to me (75) from the total range of the cardinal. Out of 187 cardinal nests examined, 113 contained eggs of the cowbird, a truly astonishing figure. This indicates how very tentative all estimates of frequency really are, as the cardinal suddenly becomes the 10th most frequently recorded host (previously estimated as the 23rd). In spite of 188 records of cowbird parasitism known to me, I do not think the cardinal is victimized more frequently than such species as Traill's flycatcher, Bell's vireo, yellow-throated vireo, or



field sparrow, for each of which the total reported instances is less than this number.

### House finch

#### *Carpodacus mexicanus* (Müller)

Recently Wauer (1964, p. 299) noted a fledgling cowbird (race *obscurus*) being fed by a house finch on June 17, 1960, in the Panamint Mountains, California. It has been noted as an occasional victim of the cowbird by a number of observers, but this is the first report that it can and does rear the young of the parasite.

### Sharp-tailed sparrow

#### *Ammospiza caudacuta* (Gmelin)

Oscar M. Root (in litt., November 1964) reported a nest with four eggs of the host and one of the brown-headed cowbird (*M. a. artemisiae*) found on June 20, 1962, in Dixon's slough, Gorrie School District, Brandon, Manitoba, by John Lane. The only previously reported instance did not give date or locality (Friedmann, 1963, p. 157).

### Lesser goldfinch

#### *Spinus psaltria* (Say)

In addition to a few records of the lesser goldfinch as a cowbird host in California (race *S. p. hesperophilus*) and one in Texas (near Austin, race *S. p. psaltria*), a second in Texas, from Beeville, has been reported (Webster, 1964).

### Lark bunting

#### *Calamospiza melanocorys* Stejneger

Since my 1963 account (p. 153), the lark bunting has been found to be a cowbird host in Saskatchewan as well as North Dakota. In 1963, near Moose Jaw, Saskatchewan, George Fairchild (in litt., November 27, 1964) found four nests of this bird, three of which were parasitized.

### Oregon junco

#### *Junco oreganus* (Townsend)

Previously known as a victim of the cowbird in British Columbia (race *J. o. montanus*) and in California (race *J. o. pinosus*), the Oregon junco has since been found parasitized near Dishman, Wash-

ington, by Rogers (1964), who reported two nests, each with two eggs of the parasite. The Washington records refer to the race *J. o. mon-tanus*. This junco is probably becoming increasingly used as a host as the cowbird expands its range in the Northwest.

### Olive sparrow

*Arremonops rufivirgata* (Lawrence)

To the few records of this sparrow as a host of the dwarf race of the brown-headed cowbird in southern Texas may be added one more, found at Beeville and reported by Webster (1964). The nest also contained eggs of the bronzed cowbird (see p. 10).

### Song sparrow

*Melospiza melodia* (Wilson)

Crossin (1965) has recorded the race *fallax* of the song sparrow as a host of the brown-headed cowbird near Tucson, Arizona. However, if the ranges of the races of the host are correctly given in the last edition of the A.U.O. checklist, we must refer this record to the race *saltonis* and not to *fallax*, just as the Wyoming record of "*fallax*" listed in my 1963 account (p. 169) must refer to *juddi*.

### Bronzed Cowbird

*Tangavius aeneus*

The following host data involves five kinds of birds not previously reported as cowbird victims. The host catalog of the bronzed cowbird now includes 56 species, or 69 species and subspecies, of birds.

### Happy wren

*Thryothorus felix* Sclater

J. Stuart Rowley (in litt.) found on July 3, 1965, about 4 miles north of Putla, Oazaca, Mexico, 3,200 feet elevation, a nest of this wren containing three eggs of its own and one of the bronzed cowbird, all nearly ready to hatch. Judging by the locality, this record must refer to the nominate race of the wren and to the southwestern race *assimilis* of the cowbird. This wren (subspecies *pallidus*) had been recorded once as a host of the bronzed cowbird (race *milleri*); the present record is therefore the first for *Thryothorus f. felix* as a host and for *Tangavius a. assimilis* as a parasite of this wren.

### Mockingbird

*Mimus polyglottos* (Linnaeus)

To the one previous report of the mockingbird (*M. p. leucopterus*) as a victim of the nominate race of the bronzed cowbird, Webster (1963, p. 471) added a nest, found at San Benito, Texas, containing the surprisingly large combination of eight eggs of the parasite and two of the host. Since mockingbirds are seldom imposed upon by either the bronzed or the brown-headed cowbird but are frequently parasitized in South America by the shiny cowbird, each additional report is an opportunity for critical study.

### Rufous-backed robin

*Turdus rufo-palliatu*s Lafresnaye

Previously unrecorded as a host of the bronzed cowbird, this robin has been found parasitized in southern Mexico. J. Stuart Rowley (in litt.) reported that on June 18, 1965, at Oaxaca City, Oaxaca, 5,000 feet elevation, he found, about 10 feet up in a small tree, a nest of this species containing three robin and two bronzed cowbird eggs. The record involves the nominate race of the host and the race *assimilis* of the parasite.

### Russet nightingale-thrush

*Catharus occidentalis* Sclater

J. Stuart Rowley (in litt.) found a nest of this thrush containing two eggs of its own and one of the bronzed cowbird at Rio Molino, near San Miguel Suchixepc, in the Sierra Madre del Sur of southern Oaxaca, Mexico, 7,300 feet elevation, on April 29, 1962. This is the first report of this thrush as a victim of the bronzed cowbird (*T. a. assimilis*). The record was published by Rowley and Orr (1964, p. 311).

### Orange-billed nightingale-thrush

*Catharus aurantiirostris* (Hartlaub)

A third record of this thrush as a host of the bronzed cowbird is reported: a nest with one egg of the host and two of the bronzed cowbird was collected 5 miles east of Cuernavaca, Morelos, May 29, 1962, by J. Stuart Rowley (see Friedmann, 1963, p. 180).

**Flame-colored tanager***Piranga bidentata* (Swainson)

This tanager has been added to the known hosts of the bronzed cowbird by Hall (1965), who saw a fledgling of the parasite, just out of the nest, being fed by a male of this host on June 24, 1959, near Rancho Miramar Chico, near Zilitla, San Luis Potosi, Mexico. On geographic grounds, this record must refer to the race *P. b. sanguinolenta* of the host and to the race *T. a. aeneus* of the parasite.

**Red ant-tanager***Habia rubica* (Vieillot)

Previously unrecorded as a victim of the bronzed cowbird, this ant-tanager was found by J. Stuart Rowley (in litt.) to be parasitized in Oaxaca, Mexico, where on June 12 and 14, 1963, he observed two such instances. One nest, found 19 miles north of Puerto Escondida, contained three eggs of the host and one of the parasite; the other, found  $2\frac{1}{2}$  miles north of San Gabriel Mixtepec, held one punctured egg of the ant-tanager, one infertile egg of the bronzed cowbird, and one egg of the latter ready to hatch. The records refer to the subspecies *H. r. affinis*, the Pacific slope race of the host, and the race *T. a. assimilis* of the parasite.

**Lichtenstein's oriole***Icterus gularis* (Wagler)

Webster (1962) notes that the bronzed cowbird has become well established around San Antonio, Texas, where it now parasitizes the race *I. g. tamaulipensis* of this oriole as well as other species of orioles. No indication is given of the number of such cases reported in that region.

**Cardinal***Richmondia cardinalis* (Linnaeus)

All previous records of the cardinal serving as host for the bronzed cowbird in eastern and southern Texas are of single or moderate numbers of eggs of the parasite. Recently Webster (1963, p. 471) cited three instances in which the intensity of parasitism was very heavy, the nests containing from six to eight cowbird eggs each. He also noted four other records, as well as Blacklock's experience in the Nueces Bay area of southern Texas, where almost every cardinal's



nest examined held one or more eggs of the bronzed cowbird. Webster's records apparently refer to the subspecies *magirostris* of the cardinal, while Blacklock's involve the race *canicauda*.

### Sclater's towhee

#### *Pipilo albicollis* Sclater

Two more instances of parasitism of this towhee by the bronzed cowbird are reported by J. Stuart Rowley, both found in Oaxaca, Mexico, in July, one in 1962 and one in 1963.

### Olive sparrow

#### *Arremonops rufivirgata* (Lawrence)

A third record of the olive sparrow as a victim of the bronzed cowbird is reported from Beeville, Texas, by Webster (1964). This instance is the same as that listed under the brown-headed cowbird in this paper, as the nest contained eggs of both species of parasites.

### Song sparrow

#### *Melospiza melodia* (Wilson)

Previously, a single race (*M. m. mexicana*) of the song sparrow was known to be victimized by the bronzed cowbird. However, Dickerman (1963) has divided the song sparrows of the Mexican plateau area into a number of races which appear, from his ample material, to be valid. The host records from Mexico City listed in my 1963 report (p. 188) must now be considered as *M. m. azteca*, while the one record from Ciudad Tlaxcala would be *M. m. mexicana*.

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